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MONOGRAPH OF THE GENUS TIQUILIA (COLDENIA, SENSU LATO), BORAGINACEAE: EHRETIOIDEAE[1]

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The genus *Tiquilia* comprises 28 taxa representing 27 species and two varieties distributed among seven sections and two subgenera. The taxa occur in the deserts of North America and South America. One species, *T. nuttallii,* occurs on both continents. Most of the species are woody; all are perennials, but some are facultative annuals.

In this treatment, *Coldenia* L. sensu A. Gray is recognized as comprising two separate genera. *Coldenia* L. is treated as a monotypic genus from southern Asia, and the genus *Tiquilia* Persoon is reinstated to accommodate the taxa occurring in xeric regions of the New World. This is the first comprehensive study of *Coldenia* and *Tiquilia.* Gray's (1862) revision treated only eight species; later studies by Johnston (1924) and Howell (1937) were fragmentary.

The conclusions here are based primarily on data from morphological, chromosomal, and ecological studies, and extensive field work. Approximately 4,000 herbarium specimens representing nearly 2,500 collections were examined. The most useful morphological characters were determined to be leaf size, shape, venation, and pubescence; calyx size and pubescence; corolla color, size, pubescence, and appendages; stamen position and length; style attachment and length; and nutlet size, shape, color, ornamentation, and attachment scar.

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Similarities of characters, such as corolla appendages or nutlet shape and ornamentation, are not always interpreted as indicating a common origin of two or more taxa. In some cases, after consideration of the total character complement, the similarities are believed to be a result of parallel evolution under similar environmental conditions.

Morphological terms used are as defined by Stearn (1966). Unusual terms, or terms for which there is some disagreement, are defined below, and illustrated in Figure 1.

Colliculate — covered with rounded projections.

Hemi-ovoid — the result of a median longitudinal division of an ovoid figure, giving two hemi-ovoid halves.

Lanceolate — narrowly elliptic.

Pusticulate — having rounded projections.

Tuberculate — having elongate or rod-shaped projections.

Most taxa were observed in the field, although the proximity of the Chihuahuan Desert made possible more thorough observations of taxa in that region during several seasons. By contrast, only one field trip was made to the Sonoran Desert, in the summer of 1971, and field observations of the South American taxa were limited to January through June, 1973. Unusual rains in South America gave growth to abnormal vegetation in some places during that period; therefore, the observations made in these localities, while useful, had to be tempered by observations of other workers, in particular, A. Weberbauer (1936). No personal field work was done in the Galapagos Islands.

A list of *Coldenia* and *Tiquilia* specimens examined is on file at TEX.

ACKNOWLEDGMENTS

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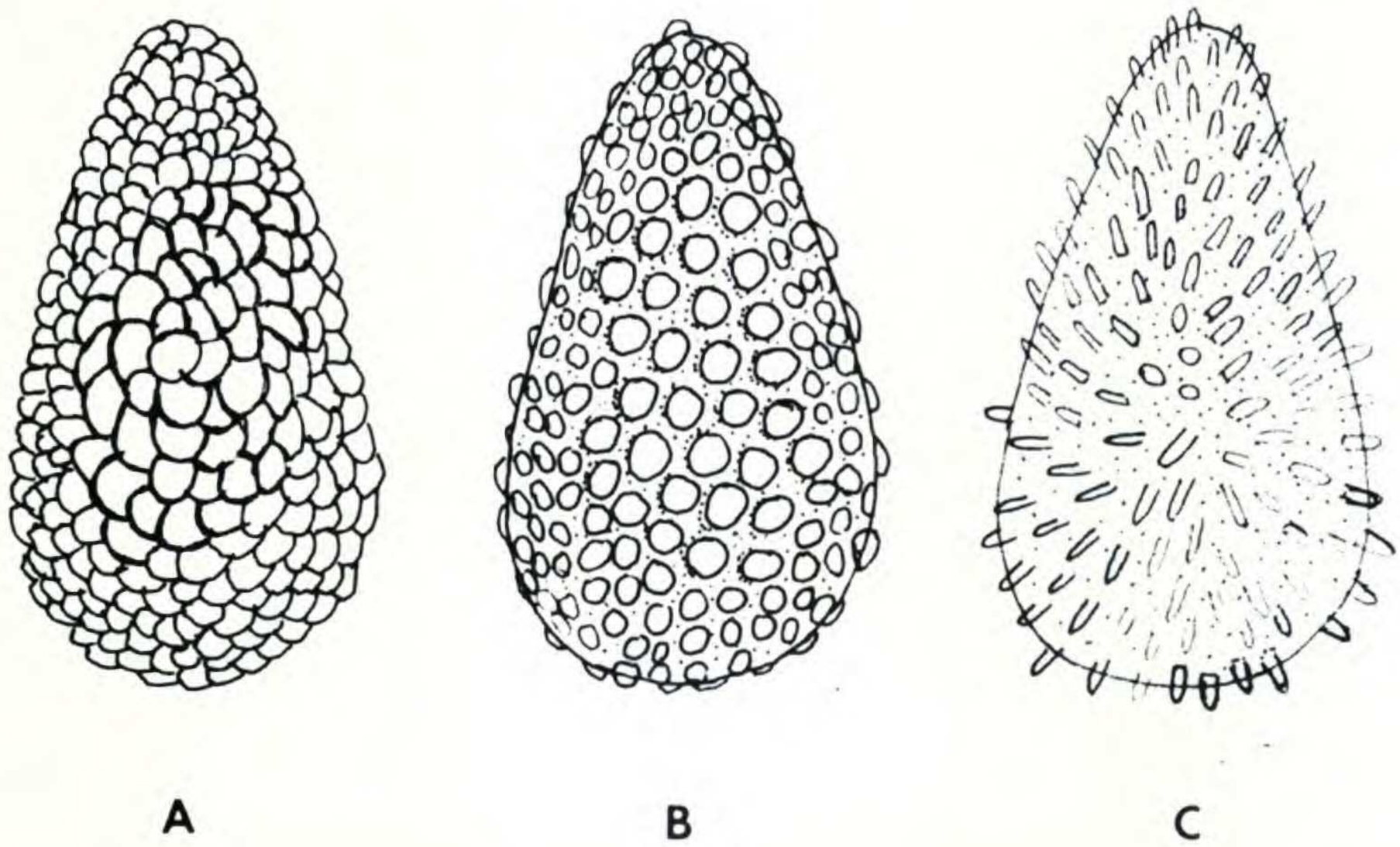

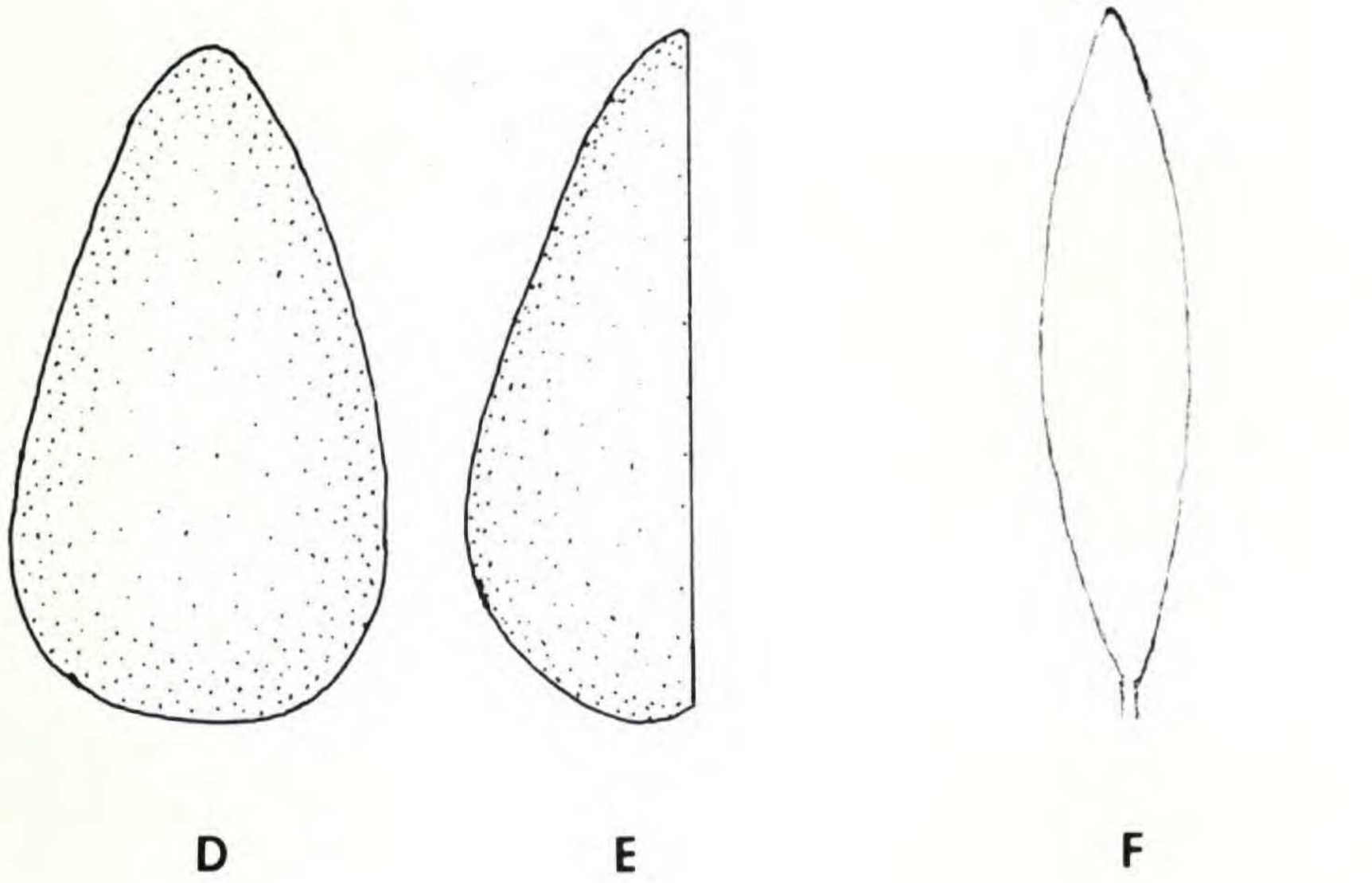

Figure 1. Illustrations of special terms. A, colliculate; B, pusticulate; C, tuberculate; D, hemi-ovoid (dorsal view); E, hemi-ovoid (lateral view); F, lanceolate.

showing me the techniques and encouraging me to proceed on my own. John Bacon, Sam Sikes, and Lowell Urbatsch offered helpful suggestions, and assistance in laboratory procedures.

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A	Arnold Arboretum, Cambridge
ARIZ	University of Arizona, Tucson.
B	Botanisches Museum, Berlin.
BA	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigaciones de las Ciencias Naturales, Buenos Aires.
BKL	Brooklyn Botanic Garden, Brooklyn.
CAS	California Academy of Sciences, San Francisco.
F	Field Museum of Natural History, Chicago.
FHO	Forest Herbarium, Oxford.
GH	Gray Herbarium, Cambridge.
HBG	Staatsinstitut für Allgemeine Botanik und Botanischer Garten, Hamburg.
JEPS	Jepson Herbarium, Berkeley.
K	Royal Botanic Gardens, Kew.
LISU	Museu, Laboratório e Jardim Botânico, Lisboa.
LL	The Lundell Herbarium of the University of Texas, Austin.
LY	Herbiers de la Faculte des Sciences de Lyon, Lyon.
MA	Instituto "Antonio José Cavanilles", Jardín Botánico, Madrid.
MEL	National Herbarium of Victoria, Royal Botanic Garden, Melbourne.
MICH	University Herbarium, University of Michigan, Ann Arbor.
NY	The New York Botanical Garden, New York.
OXF	Fielding Herbarium, Druce Herbarium, Oxford.
POM	Herbarium of Pomona College, Claremont.
RM	Rocky Mountain Herbarium, Laramie.
RSA	Rancho Santa Ana Botanic Garden, Claremont.
TEX	The University of Texas Herbarium, Austin.
UC	Herbarium of the University of California, Berkeley.
US	U. S. National Museum, Washington, D. C.

TAXONOMIC HISTORY

The genus *Coldenia* was described by Linnaeus (1753) and named to honor Cadwallader Colden, a correspondent of Linnaeus and then Lieutenant-governor of the colony of New York (Gray, 1888). A single Old World species, *C. procumbens,* was treated.

Ruiz and Pavon (1799) described *Lithospermum dichotomum,* which they collected in Peru, and subsequently, Persoon (1805) established the genus *Tiquilia* to accommodate this taxon, the generic name being derived from the vernacular name, reported by Ruiz and Pavon (1799) as "Tiquil-tiquil". It is possible that the cited vernacular name is simply a corruption of the Quechua word for flower, "t'ika" (Pers. comm., Helen Barler, April, 1975; Lira, 1973).

Rafinesque (1836) contributed a superfluous generic name, *Monomesia,* based on an unnamed specimen collected by Dombey which had been described in passing by Jussieu (1789) as a possible congener of *Coldenia.* J. D. Hooker (1847) described the genus *Galapagoa* in his treatment of two new species from the Galapagos Islands, and Torrey and Gray (1857), working with specimens collected on an expedition to determine a railroad route from the Mississippi River to the Pacific Ocean, described three monotypic genera, viz. *Eddya, Ptilocalyx,* and *Stegnocarpus.*

The first revisionary treatment of the genus was published as a footnote in a paper on an unrelated subject by Gray (1862). Dealing with only eight species, he combined *Eddya, Ptilocalyx, Stegnocarpus,* and *Tiquilia* with *Coldenia,* but noted, "Those who regard the reduction here foreshadowed as too great, might be better satisfied with three genera, viz. *Coldenia, Ptilocalyx,* and *Tiquilia.*" Five sections were recognized: *Eucoldenia* (*Coldenia procumbens*); *Stegnocarpus* (*C. canescens, C. greggii*); *Eddya* (*C. hispidissima*); *Tiquilia* (*C. dichotoma, C. darwinii, C. fusca*); and *Tiquiliopsis* (*C. nuttallii*).

Bentham and Hooker (1876) and Gürke (1891) followed Gray's broader circumscription of *Coldenia.* Heller (1906), however, evidently preferring a narrower circumscription of the genus, transferred *Coldenia nuttallii* Benth. ex Hook. to a new genus, *Tiquiliopsis.*

Johnston (1924), in a revisionary treatment of *Coldenia,* followed Gray but recognized only three of Gray's sections: *Eucoldenia,*

Table 1. **Classification of Coldenia Summarized from I. M. Johnston.**

Section **Eucoldenia** DC.
Series COLDENIA
C. procumbens L.
"Series" STEGNOCARPUS DC. (sic.)
C. canescens DC.
C. greggii (Torrey & Gray) Gray
"Series" TIQUILIA Gray (sic.)
C. dichotoma (Persoon) Gray
C. grandiflora Phil.
Section **Eddya** Gray
C. darwinii (Hooker f.) Gray
C. paronychioides Phil.
C. hispidissima (Torrey & Gray) Gray
C. tomentosa Watson
C. mexicana Watson
C. purpusii Brandeg.
C. cuspidata I. M. Johnston
Section **Sphaerocarya** I. M. Johnston
C. litoralis Phil.
C. atacamensis Phil.
C. parviflora Phil.
Section **Tiquiliopsis** Gray
C. nuttallii Bentham
C. palmeri Gray
C. plicata (Torrey) Coville

Eddya, and *Tiquiliopsis.* Sects. *Stegnocarpus* and *Tiquilia* were reduced to series of sect. *Eucoldenia.* Another section, *Sphaerocarya,* was designated to accommodate the taxa with spheroidal nutlets. Limiting his treatment to morphological evidence, Johnston interpreted similarity of critical characters, such as nutlet shape and presence or absence of corolla appendages, as an indication of phyletic relationships. He treated disjunct and sympatric taxa without regard to their geography, producing a confused phyletic scheme. His treatment is summarized in Table 1.

Howell (1937), in a treatment of the coldenias from the Galapagos Islands, also followed Gray's generic disposition. Most recent publications, such as floras, descriptions of new species, or clarification of established species, have followed Gray, establishing a single genus encompassing the Old World and New World taxa.

The major deviation of the present treatment from that of Gray (1862) and Johnston (1924) is the separation of the Old World and New World taxa into two genera; these genera are compared in the section on generic relationships. In addition, there is some intersectional rearrangement, and a significant number of species has been added. *Coldenia* L. is treated as a monotypic Old World genus, and *Tiquilia* Persoon is reinstated to accommodate the New World taxa. *Tiquilia* is divided into two subgenera and seven sections. Keys and descriptions are included in the section on taxonomy. The proposed classification is given in Table 2.

GENERIC RELATIONSHIPS

Coldenia sensu Gray (1862) historically has been treated as a member of subfam. Ehretioideae by various workers (Bentham & Hooker, 1876; Gürke, 1891; Johnston, 1951). The once-cleft style, its generally apical position on the fruit, and the two stigmas not differentiated into sterile and receptive tissue have served as the principal key characters relating it with this subfamily. A key to the subfamilies of the Boraginaceae, modified from Johnston (1951), is presented below.

KEY TO THE SUBFAMILIES OF BORAGINACEAE

a. Style twice forked, the 4 branches each bearing a stigma; cotyledons plicate. ..... Cordioideae.

a. Style simple or once divided; stigmas 1 or 2; cotyledons not plicate. ..... b.

b. Style borne directly on the fruit, seated terminally in its pericarp, falling away with it; style simple or once divided; endosperm usually present though often meager. ..... c.

b. Style not borne directly on the fruit, seated independently at the middle of the floral receptacle or gynobase, arising between the nutlets and free from them; style simple; stigma simple or rarely 2-lobed; endosperm usually absent; mostly herbs. ..... Boraginoideae.

c. Style usually lobed or parted; stigmas usually 2, small, capitate or elongate or rarely sub-peltate, not differentiated into receptive and sterile tissue. ..... Ehretioideae.

c. Style simple or none; stigma single, partially sterile, conic or frustrum-like or rarely peltate, stigmatic only in a sharply delimited, usually tumid circumferential band at the base, or rarely irregularly globose and broadly and somewhat indefinitely stigmatic laterally but sterile at the apex; sterile portion of stigma frequently bilobed. ..... Heliotropioideae.

Table 2. **Classification of Tiquilia.**

Subgenus **Eddya** subg. nov. TYPE: *Tiquilia hispidissima* (Torrey & Gray) A. Richardson.

Folia margine integra; petioli breves elliptico-rectangulares vel filiformes. Mericarpia ovata vel obpyriformia vel fructus sphaeroideus mericarpiis 4, cicatricibus stylorum apicalibus. Chromosomatum numerus basalis $x = 9$.

Section STEGNOCARPUS (DC.) A. Richardson, comb. nov.

T. canescens (DC.) A. Richardson

var. *canescens*

var. *pulchella* (I. M. Johnston) A. Richardson

Section PTILOCALYX A. Richardson, sect. nov.

Frutices erecti ad 1.0 m. alti. Inflorescentia terminalia bracteata globosa. Calyces plumosi decidui. Fructus mericarpio solitario in calyce remanenti.

T. greggii (Torrey & Gray) A. Richardson

Section EDDYA Gray

T. latior (I. M. Johnston) A. Richardson

T. hispidissima (Torrey & Gray) A. Richardson (Type)

T. turneri A. Richardson

T. tuberculata A. Richardson

T. mexicana (Watson) A. Richardson

T. gossypina (Wooton & Standley) A. Richardson

T. purpusii (Brandeg.) A. Richardson

Subgenus **Tiquilia** TYPE: *Tiquilia dichotoma* Persoon

Section TIQUILIOPSIS (Gray) A. Richardson, comb. nov.

T. nuttallii (Bentham) A. Richardson (Type)

T. plicata (Torrey) A. Richardson

T. cuspidata (I. M. Johnston) A. Richardson

T. palmeri (Gray) A. Richardson

Section TIQUILIA

T. dichotoma Persoon (Type)

T. simulans (I. M. Johnston) A. Richardson

T. grandiflora (Phil.) A. Richardson

T. ferreyrae (I. M. Johnston) A. Richardson

Section SPHAEROCARYA (I. M. Johnston) A. Richardson, comb. nov.

T. atacamensis (Phil.) A. Richardson

T. tacnensis A. Richardson

T. litoralis (Phil.) A. Richardson (Type)

T. elongata (Rusby) A. Richardson

T. hunteri A. Richardson

T. conspicua (I. M. Johnston) A. Richardson

Section GALAPAGOA sect. nov.

Table 2 (Continued)

Laminae foliorum ovatae vel obovatae. Petioli ovato-trullati. Mericarpia ovata ventraliter ab imo ad summum affixa cicatricibus longissimis. Cicatrices stylorum apicales vel subapicales.

T. paronychioides (Phil.) A. Richardson
T. galapagoa (J. T. Howell) A. Richardson
T. nesiotica (J. T. Howell) A. Richardson
T. darwinii (Hooker f.) A. Richardson (Type)

Although *Coldenia* sensu Gray fits better with the Ehretioideae than with any other subfamily, it is strikingly atypical. Johnston (1951) noted that it was clearly a member of the Ehretioideae although the relationships are not close. The following differences exist between *Coldenia* sensu Gray and other genera of the Ehretioideae:

COLDENIA SENSU GRAY	OTHER EHRETIOIDEAE
1. Herbaceous to woody; usually prostrate, or sub-erect; 1 species erect, 1 meter tall or less.	1. Trees or erect shrubs.
2. Inflorescences crowded, or reduced to 1 or few flowers.	2. Inflorescences open, distinct scorpioid cymes.
3. Fruit dry, of 4 nutlets.	3. Fruit a drupe.

In addition to the above characteristics, style attachment and leaf venation are distinctive. In the New World taxa, style attachments are apical, subapical, sub-basal, basal, or gynobasic; this latter condition brings to mind subfam. Boraginoideae.

In taxa with lobed leaves, the lateral veins run from the midrib to the sinuses rather than to the apices of the lobes. This feature was noted by DeCandolle (1845), who found this condition duplicated only in *Crataegus oxyacantha* (Rosaceae) and in species of *Rhinanthus* (Scrophulariaceae). Johnston (1951) stated that in these two taxa only an occasional or secondary vein behaved in this manner whereas in *Coldenia* all lateral veins go to the sinuses. He described this condition as unorthodox and perhaps unique.

The present investigation confirms Johnston's conclusions regarding *Crataegus oxyacantha;* however, in the opinion of the present writer, at least four species of *Rhinanthus* (*R. crista-galli, R. greenlandicus, R. major,* and *R. minor*) duplicate the venation of *Coldenia.*

Coldenia sensu Gray separates into two genera with distinct characters and without intermediates. In a recent paper (Richardson, 1976) the New World genus *Tiquilia* Persoon is reinstated and *Coldenia* L. is recognized as a monotypic Old World genus. *Tiquilia* Persoon is comprised of perennial, usually woody plants without adventitious roots, and with symmetrical leaves and pentamerous flowers solitary or in clusters, axillary or subtended by bracts. It occupies xeric regions of the New World. *Coldenia* L. is comprised of an herbaceous annual with adventitious roots, asymmetrical leaves, and tetramerous flowers, solitary, extra-axillary, not subtended by bracts. It occupies forest and woodland riverbanks and dried rice fields of the Old World. *Coldenia* is treated below.

Coldenia L., Sp. Pl. **1:** 125. 1753.

Lobophyllum F. Mueller, Hooker's Jour. Bot. Kew Gard. Misc. **9:** 21. 1857.

Prostrate annual herbs. Leaves alternate, blades obovate, distinctly asymmetric, the margins crenate or lobed, the veins terminating at the sinus bases. Flowers solitary, sub-sessile, extra-axillary, 4-merous. Styles 2. Fruit spheroid, of 4 nutlets.

Coldenia procumbens L. Sp. Pl. **1:** 125. 1753. (Holotype: L, No. 174.1, not seen. Photograph, TEX!).

Lobophyllum tetrandrum F. Mueller, Hooker's Jour. Bot. Kew Gard. Misc. **9:** 21. 1857. TYPE: **Australia.** VICTORIA: Sturt Creek, on periodically inundated banks of rivers and streams, March 1856, *Mueller s.n.* (Holotype, K. not seen. Isotype, MEL!).

Coldenia angolensis Welw., Ann. do Cons. Ultramarino **1:** 527–592. 1859. TYPE: **Africa.** ANGOLA: Barra do Dande district near Bombo, Sept. 1858, *Welwitsch 5445* (Holotype, LISU!).

Stems branching, slender (Figure 2), 1.0–5.5 mm. thick, villous with hairs ca. 1.0 mm. long, sometimes bearing adventitious roots. Leaf blades (Figure 3A) 1.0–3.3 cm. long, 0.6–1.8 cm. across; upper surfaces with appressed straight hairs to 1.0 mm. long converging on the medians between the veins and flowing toward the margins; lower surfaces villous or with spreading hairs ca. 1.0 mm. long

Figure 2. Drawing of habit of *Coldenia procumbens*.

especially along the veins; petioles 0.2–0.9 cm. long with spreading hairs ca. 1.0 mm. long. Calyces ca. 1.5 mm. long, lobes unequal, lanceolate to ovate, joined at or near the base, with apically appressed hairs to 1.0 mm. long on inner and outer surfaces. Corollas sometimes scented, white to yellowish white, campanulate, minute, 1.3–2.0 mm. long. Stamens included, adnate to the corollas about the mid-point, alternate with the lobes; filaments ca. 0.3 mm. long. Styles united basally. Fruit (Figure 3B) spheroid, 2.2–4.8 mm. across, lobed, puberulent and spined, apical spines overtopping the styles; mericarps 4, joined into pairs by a thick ridge, a pronounced sulcus at right angles to the ridge marking the unions of the pairs, each mericarp having one large and one small commisural face (Figure 3C).

DISTRIBUTION: Mainly in southeastern and southwestern Asia, northeastern Africa, Madagascar, and northern Australia (Figure 4). *Coldenia procumbens* is commonly found growing on river banks that have been inundated, or on dried-up rice paddies. The nutlets float, making them ideally suited for dispersal by water. It is likely that much of the Old World distribution of this taxon has been brought about by man as the plants are often associated with rice fields.

Coldenia procumbens blooms throughout the year.

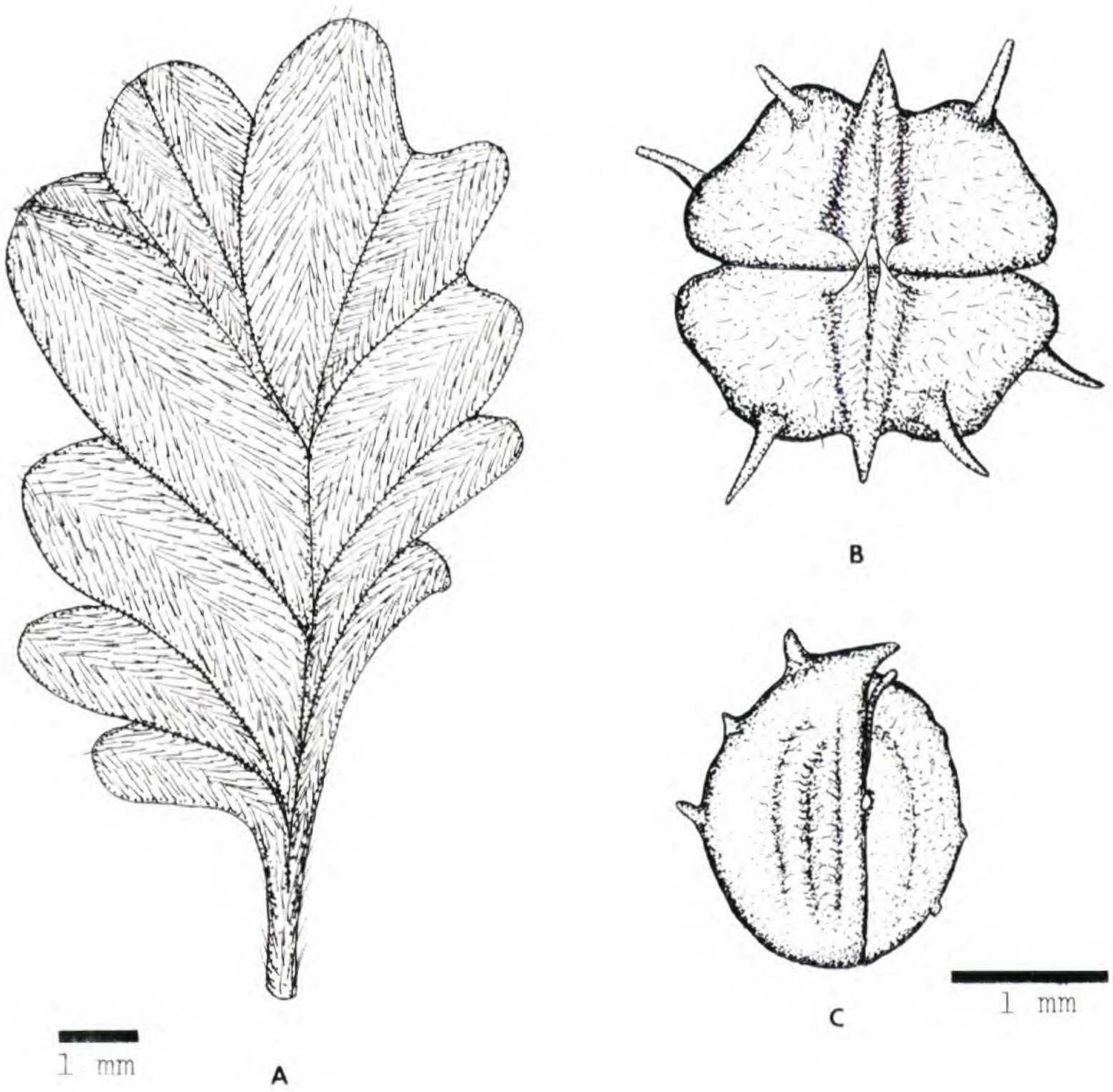

Figure 3. *Coldenia procumbens*. A, leaf; B, fruit; C, nutlet.

CHROMOSOMAL STUDIES

Little work has been done on the chromosomes of sub-fam. Ehretioideae. Chromosome counts have been reported for only three genera: *Ehretia*, *Cortesia*, and *Coldenia*. The first counts reported were by Britton (1951), for three species of *Ehretia*. He counted *E. anacua*, $2n = 40$, *E. microphylla*, $2n = 32$, and *E. thyrsiflora*, $2n = 32$. Since all the numbers are multiples of eight, he proposed $x = 8$ as the base number for the subfamily. In the same work, on the basis of counts of 90 species and varieties representing 19 genera, he proposed $x = 8$ as the base number for the Boraginaceae. Subsequently, Chuang *et al.* (1963) reported *Ehretia dicksonia* as $n = 30$; Bhattacharya (1968) reported $n = 15$ for *E. acuminata;* and Baquar and Askari (1970, 1970a) reported *E. as-*

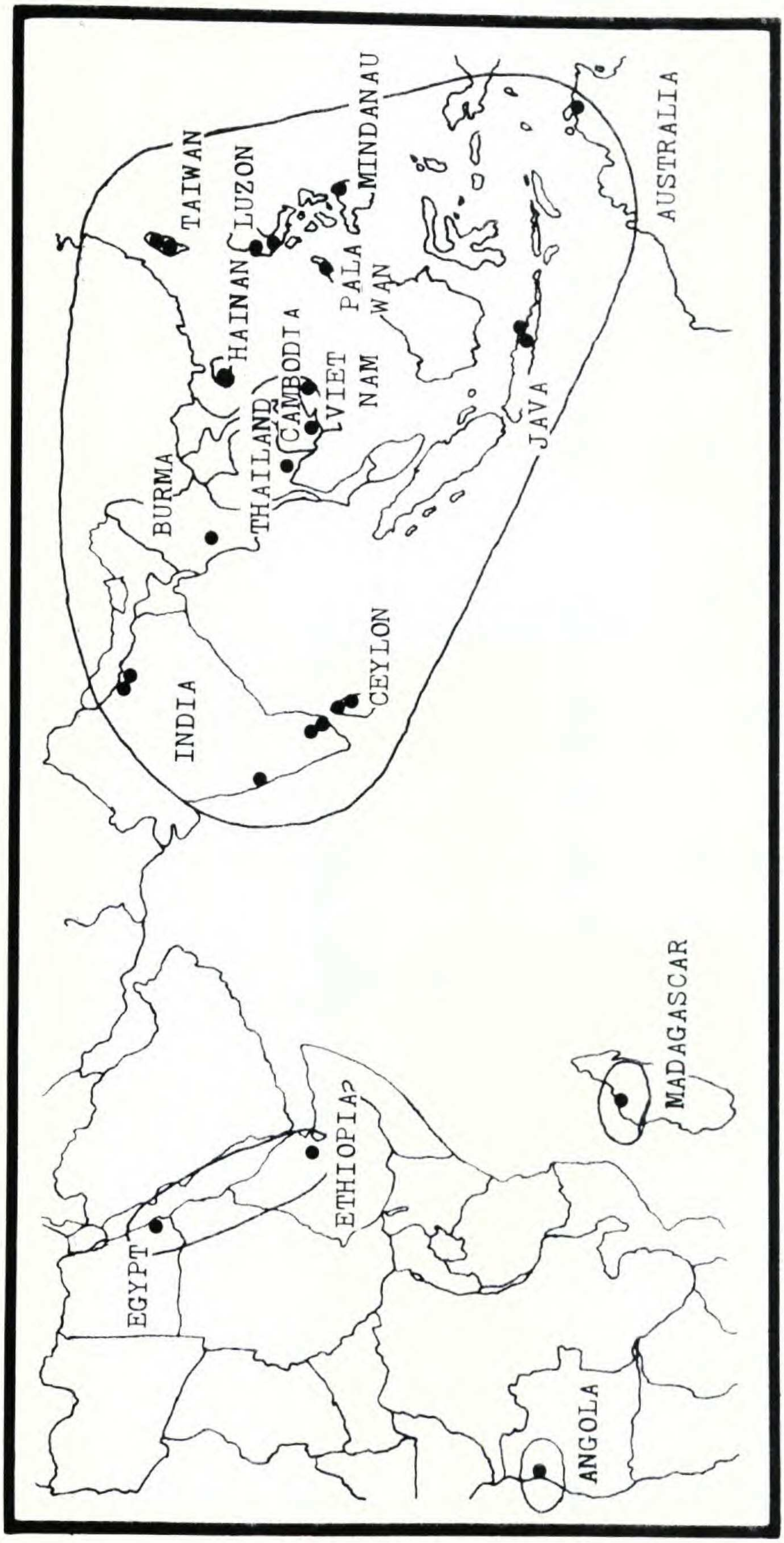

Figure 4. Distribution of *Coldenia procumbens*.

pera as $n = 8$. These counts seem to support Britton's hypothesis of a base number of $x = 8$. However, Di Fulvio (1965) found *Cortesia cuneifolia* to be $2n = 18$, suggesting the possibility of a base number of $x = 9$.

Chromosome numbers for *Coldenia* sensu lato were published by Chisaki (1959). He reported *C. canescens* and *C. purpusii* to have $n = 9$, and *C. palmeri* and *C. plicata* with $n = 8$. No further counts have been published.

During this investigation bud material was collected in the field for meiotic counts and placed in a modified Carnoy's fluid (4 parts chloroform : 3 parts absolute ethanol : 1 part glacial acetic acid), and stored in the refrigerator until the counts were made. Aceto-carmine stain was used.

A relatively low number of buds was successfully counted. The small size of the buds in the desirable stages of meiosis made necessary the use of a microscope to dissect them from the enclosing leaves, bracts, or bud clusters. Consequently, it was impossible to readily select buds of the proper size in the field; instead, actively growing, flowering sections of the plants were selected in the hope that some countable buds would be present. No correlation was noted between the time the buds were collected and the stage of meiosis. Most cells counted were in early anaphase. Counts were made for 81 populations, representing 22 of the 27 species. The results are listed in Table 3. Vouchers are deposited at TEX.

Two base numbers are readily recognized: $x = 9$ and $x = 8$. On the basis of distinctive morphology and distribution as well as chromosome number, two subgenera are recognized: Subg. *Eddya* with a base chromosome number where $x = 9$, and subg. *Tiquilia* where $x = 8$. Within subg. *Eddya,* chromosome numbers are not of taxonomic importance as all species have the same haploid number, $n = 9$. However, one aneuploid individual, $n = 8$, was growing in a population of *Tiquilia purpusii* from which a count of $n = 9$ was also made. Bud material was collected again from that population but no meiotic microsporocytes were found. Since all other populations counted had $n = 9$, that number is most likely predominant in the population. Whether the $n = 8$ count represents one aberrant individual or a number of individuals is not known. It is believed, however, that the count is accurate.

Chromosome numbers have been useful in determining relationships in subg. *Tiquilia.* The single North American section, *Tiquili-*

Table 3. **Species of Tiquilia Examined for Chromosome Number.**

Species	*n* number	Location and Voucher
Subgenus **Eddya**		
Section STEGNOCARPUS		
T. canescens var. *canescens*	9	**Arizona:** COCONINO CO. S rim of Grand Canyon. *Raven 13122*[a]*
	9	**Mexico:** COAHUILA. 17.1 mi. E of Musquiz. *Richardson 1587A.*
	9	**Mexico:** COAHUILA. Hwy. 57, 27.8 mi. S of Nuevo Rosita road. *Richardson 1589A.*
Section PTILOCALYX		
T. greggii	ca. 9	**Mexico:** CHIHUAHUA. Ca. 18 mi. S of Ojinaga. *Richardson 1472D, 1472E.*
	9	**Mexico.** CHIHUAHUA. 25.1 mi. N of Aldama. *Richardson 1602A, 1602B,* and *1602C.*
	9	**Mexico:** CHIHUAHUA. 50 mi. N of Aldama. *Richardson 1609B.*
Section EDDYA		
T. latior	9	**Arizona:** COCONINO CO. Lee's Ferry. *Sanderson 428.*
T. hispidissima	9	**New Mexico:** OTERO CO. White Sands. *Richardson 1613A, 1613B.*
	9	**Texas:** BREWSTER CO. 42.5 mi. S of Marathon. *Bacon 954.*
	9	**Mexico:** CHIHUAHUA. 11.2 mi. SE of hwy. 16 from Aldama on road to Pasado El Granjero. *Richardson 1605A, 1605B, 1605E.*
	ca. 9	**Mexico:** CHIHUAHUA. 50 mi N of Aldama. *Richardson 1606B.*
T. turneri	9	**Mexico:** COAHUILA. 12.4 mi. S, 2 mi. W of Cuatro Ciénegas. *Richardson 1595E, 1595F.*
T. mexicana	ca. 9	**Mexico:** CHIHUAHUA. Ca. 11 mi. S of Ojinaga. *Richardson 1465.*

Table 3 (Continued)

Species	*n* number	Location and Voucher
	9	**Mexico:** COAHUILA. 33 mi. W of Saltillo. *Richardson 1572E, 1572F.*
	9	**Mexico:** COAHUILA. 18.6 mi. S of Cuatro Ciénegas. *Richardson 1598A, 1598B, 1598C.*
T. gossypina	ca. 9	**Mexico:** CHIHUAHUA. 50 mi. N of Aldama. *Richardson 1608B.*
	ca. 9	**Mexico:** CHIHUAHUA. 50 mi. N of Aldama. *Richardson 1610B.*
	ca. 9	**Mexico:** CHIHUAHUA. 137.9 mi. N of Camargo. *Richardson 1672–10, 1672–14.*
	ca. 9	**Mexico:** COAHUILA. 40 km. N of Monclova. *Richardson 1429A.*
	ca. 9	**Mexico:** COAHUILA. 4.4 mi. W of Paila. *Richardson 1577A, 1577B, 1577D.*
	9	**Mexico:** COAHUILA. 31 mi. N of San Pedro de las Colonias. *Richardson 1581A, 1581B.*
	9	**Mexico:** COAHUILA. 64.1 mi. N of San Pedro de las Colonias. *Richardson 1584A.*
	9	**Mexico:** COAHUILA. 39 km. N of Monclova. *Richardson 1593B.*
	9	**Mexico:** COAHUILA. 39 km. N of Monclova. *Richardson 1594B.*
	9	**Mexico:** COAHUILA. 65.3 mi. N of San Pedro de las Colonias. *Richardson 1652–11.*
	ca. 9	**Mexico:** COAHUILA. 36.1 mi. N of San Pedro de las Colonias. *Richardson 1656B.*
	ca. 9	**Mexico:** COAHUILA. 36.1 mi. N of San Pedro de las Colonias. *Richardson 1657E.*

Table 3 (Continued)

Species	*n* number	Location and Voucher
T. purpusii	9	**Mexico:** NUEVO LEON. 5.5 mi. S of José Maria Aguirre. *Moran 6320*[b].
	9	**Mexico:** NUEVO LEON. 20.2 mi. N of Matehuala. *Richardson 1695B.*
	9	**Mexico:** SAN LUIS POTOSÍ. Hwy. 80, 16.6 mi. E of junction with hwy. 101. *Richardson 1525.*
	9, 8	**Mexico:** SAN LUIS POTOSÍ. Road to Guadalcazar, at junction with hwy. 57. *Richardson 1541.*
	9	**Mexico:** SAN LUIS POTOSÍ. 5 mi. N of La Ventura. *Richardson 1543A, 1543B.*
	9	**Mexico:** SAN LUIS POTOSÍ. Cerritos road, 5 mi. from junction with hwy 57. *Richardson 1551.*
	9	**Mexico:** SAN LUIS POTOSÍ. 25 mi. W of Ciudad Maiz. *Richardson 1691B, 1691C, 1691E.*
	9	**Mexico:** SAN LUIS POTOSÍ. Hwy. 57, 39.7 mi. N of intersection with hwy 80. *Richardson 1693A.*
	9	**Mexico:** TAMAULIPAS. 50 mi. SW of Victoria. *Richardson 1519.*
Subgenus **Tiquilia**		
Section TIQUILIOPSIS		
T. nuttallii	8	**California:** INYO CO. Bishop Creek. *Raven 14306*[c].
T. plicata	8	**Arizona:** YUMA CO. Yuma. *Richardson 1628.*
	8	**California:** IMPERIAL CO. Junction hwys. 80–98 and road from Ogilby. *Alava 1809*[d].
	8	**California:** IMPERIAL CO. Ca. 20 mi. E of Winterhaven. *Bacon 922A.*

Table 3 (Continued)

Species	*n* number	Location and Voucher
	8	**California:** RIVERSIDE CO. Palm Springs. *Bacon 939A, 939B, 939D.*
	8	**California:** RIVERSIDE CO. 51.6 mi. E of 29 Palms. *Bacon 942A, 942B, 942D.*
	ca. 8	**California:** RIVERSIDE CO. 51.6 mi. E of 29 Palms. *Bacon 942C.*
	8	**California:** SAN DIEGO CO. 29 mi. W of Ocotillo. *Bacon 935A, 935B, 935C, 935D.*
	8	**California:** SAN DIEGO CO. 1 mi. N of hwy. 76, Ocotillo road to Borrego Springs. *Bacon 937B, 937D.*
	8	**California:** SAN DIEGO CO. 12.3 mi. W of hwy. S-78 from junction of hwys. S-86 and S-78. *Bacon 938A.*
	8	**Mexico:** BAJA CALIFORNIA. 57 mi. S of Mexicali. *Bacon 923A, 923B, 923C.*
	8	**Mexico:** SONORA. Desemboque. *Richardson 1620.*
T. cuspidata	8	**Mexico:** BAJA CALIFORNIA. 70 mi. S of Mulege. *Hartman & Seaman 3266.*
	8	**Mexico:** SONORA. Km. 95 between Hermosilla and Bahia Kino. *Richardson 1616.*
T. palmeri	8	**Arizona:** YUMA CO. Yuma. *Bacon 921A, 921B, 921C.*
	8	**California:** IMPERIAL CO. Junction of hwys. 8 and S-2. *Bacon 934A, 934B.*
	9	**California:** IMPERIAL CO. Junction of hwys. 8 and S-2. *Bacon 934C.*
	8	**California:** RIVERSIDE CO. 27 mi. S of Vidal. *Alava 1831*[c].

Table 3 (Continued)

Species	*n* number	Location and Voucher
	8	**California:** RIVERSIDE CO. 35.4 mi. S of Vidal. *Bacon 944A, 944B, 944C.*
	8	**California:** SAN DIEGO CO. 8 mi. W of Ocotillo. *Bacon 936.*
	8	**California:** SAN DIEGO CO. 1 mi. N of hwy. 76, Ocotillo road to Borrego Springs. *Bacon 937A, 937C.*
	9	**California:** SAN DIEGO CO. 1 mi. N of hwy. 76, Ocotillo road to Borrego Springs. *Bacon 937E.*
	8	**Mexico:** BAJA CALIFORNIA. 31.3 mi. S of Puertocitos. *Bacon 924A, 924C.*
	8	**Mexico:** BAJA CALIFORNIA. 39.7 mi. S of Puertocitos. *Bacon 925B, 925C.*
	8	**Mexico:** BAJA CALIFORNIA. 59 mi. S of Puertocitos. *Bacon 926B, 926C.*
	8	**Mexico:** SONORA. 20 mi. W of Sonoita. *Richardson 1622.*
	8	**Mexico:** SONORA. 95 km. W of Sonoita. *Richardson 1625A.*
Section TIQUILIA		
T. dichotoma	16	**Peru:** ICA. 383 km. S of Lima. *Richardson 2098.*
T. simulans	16	**Peru:** AREQUIPA. 129 km. N of Camaná. *Richardson 2150.*
	16	**Peru:** AREQUIPA. 2 km. E of Puerto Lomas. *Richardson 2154.*
T. grandiflora	16	**Peru:** AREQUIPA. 30 km. W of Arequipa on Cerro Verde road. *Richardson 2124.*
T. ferreyrae	16	**Peru:** AREQUIPA. 72 km. SW of Nazca. *Richardson 2100.*

Table 3 (Continued)

Species	*n* number	Location and Voucher
Section SPHAEROCARYA		
T. tacnensis	16	**Peru:** TACNA. 70 km. N of Tacna. *Richardson 2130.*
	16	**Peru:** TACNA. 51 km. n of Tacna. *Richardson 2138.*
T. elongata	ca. 16	**Peru:** AREQUIPA. 76 km. SE of Camaná. *Richardson 2112.*
	16	**Peru:** AREQUIPA. 99 km. SE of Camaná. *Richardson 2115.*
	ca. 16	**Peru:** AREQUIPA. 19 km. N of Arequipa. *Richardson 2117.*
	ca. 16	**Peru:** AREQUIPA. Yura. *Richardson 2119.*
	ca. 16	**Peru:** AREQUIPA. Outside Arequipa, slopes of Chachani. *Richardson 2120.*
T. hunteri	14	**Peru:** AREQUIPA. 714 km. S of Lima between Chala and Camaná. *Richardson 2106.*
T. litoralis	15	**Chile:** ANTOFAGASTA. Pan American hwy., near turnoff to Taltal. *Richardson 2173.*
	ca. 15	**Chile:** ATACAMA. S of Copiapó. *Richardson 2179.*
T. conspicua	16	**Peru:** AREQUIPA. Mollendo. *Richardson 2126.*
	16	**Peru:** AREQUIPA. Mollendo. *Richardson 2140.*
Section GALAPAGOA		
T. paronychioides	ca. 14–16	**Peru:** PIURA. 100 km. S of Talara. *Richardson 2050.*

*Superscript letters refer to counts made from the following sources:
[a]Cave (1959); voucher at UC.
[b]Chisaki (1959); voucher at UC.
[c]Chisaki (1960, not published); voucher at UC.
[d]Chisaki (1959); voucher at JEPS.
[e]Chisaki (1959); voucher at JEPS.

opsis, is diploid with $n = 8$. Of particular note is *Tiquilia palmeri*. Chromosome counts were made from eleven populations of this species. Nine of them were $n = 8$. The remaining two populations were found to have aneuploids. In each case, two individuals were counted $n = 8$ and one was $n = 9$. No significant corresponding morphological differences were detected between the diploids and aneuploids.

Tiquilia nuttallii, also in sect. *Tiquiliopsis*, is poorly known chromosomally. This is the only species occurring on both American continents. Only one count from North America, $n = 8$ (Chisaki, 1960), has been reported. Unfortunately no South American populations have been counted. Since specimens from the two continents are indistinguishable morphologically, and they have similar flavonoid chromatograph patterns (Richardson, 1975, unpublished), it seems likely that the chromosome numbers are the same. More counts are needed of populations from both continents.

The remaining three sections are South American in distribution, and all are polyploids, the predominant haploid number being $n = 16$. Two of the more advanced species, *Tiquilia litoralis* and *T. hunteri* (sect. *Sphaerocarya*), have derived haploid numbers of $n = 15$ and $n = 14$ respectively.

The tetraploids could have arisen by one of the following methods. (1) There was a single introduction of a tetraploid from North America. However, there are no tetraploids known from North America. (2) Diploids were introduced from North America. Subsequent doubling of the chromosome complement produced a population better adapted to the South American deserts, and the less well-adapted diploids failed to survive. This is not to imply that tetraploids are necessarily better adapted to a given habitat than diploids, although this condition has been observed (Grant, 1971, p. 248).

Whether the polyploids originated as alloploids or as autoploids is not known. Alloploids could have arisen by hybridization and subsequent doubling of the chromosome complement. Autoploids could have arisen by somatic doubling in mitosis or by nonreduction in meiosis (Grant, *op. cit.*). If the ancestral polyploids were autoploids, diploidization has occurred since (Brown & Bertke, 1969, p. 497), and so the species are properly called amphidiploids. Meiotic pairing is regular, and no multivalents have been observed.

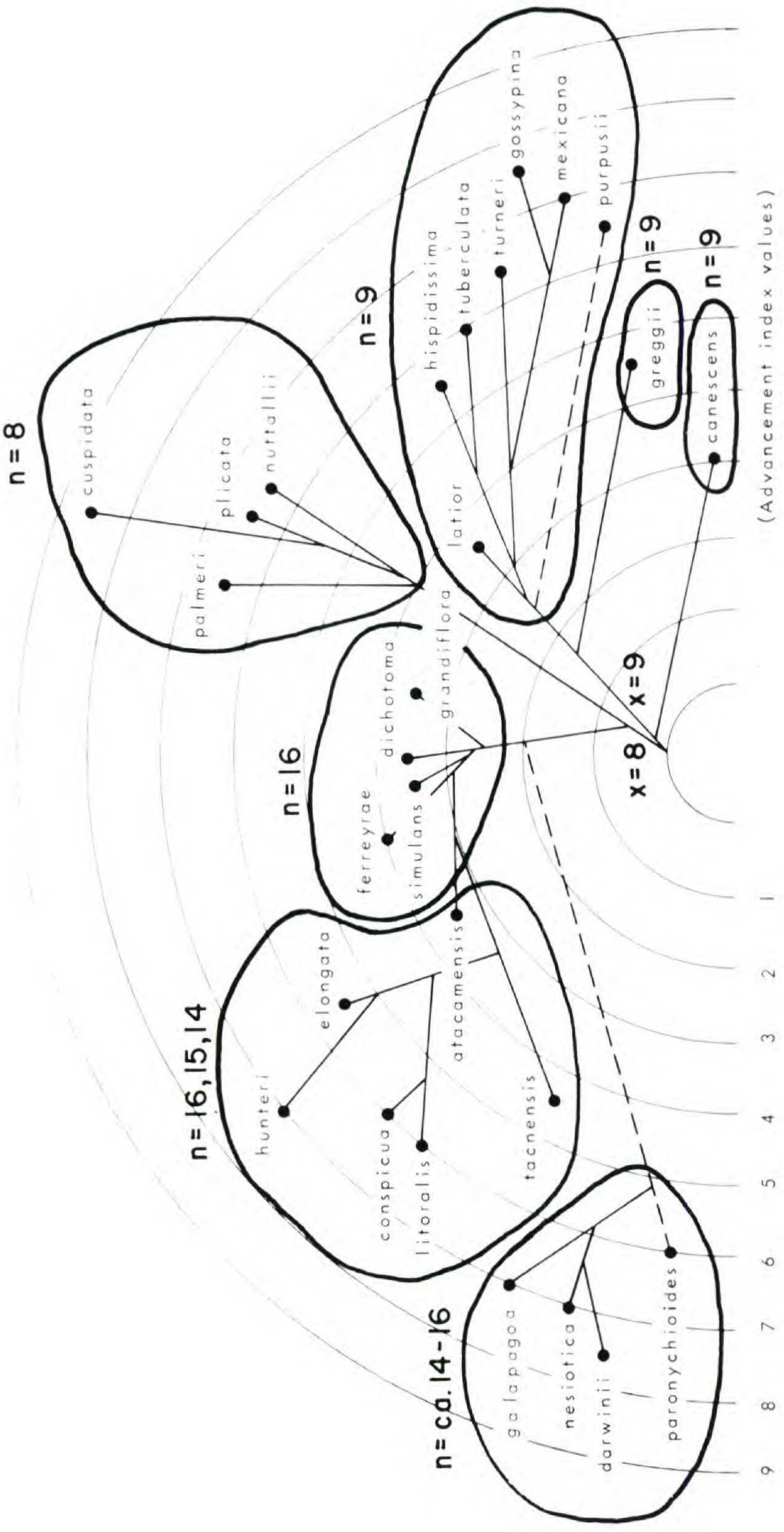

Figure 5. Diagram of species relationships and degree of advancement in *Tiquilia*.

No chromosome numbers are known for the species of sect. *Galapagoa,* excepting *Tiquilia paronychioides* which has been counted as n = ca. 14–16. Although limited in its usefulness, the information has served to identify the species as polyploid. More chromosome counts of *T. paronychioides* and the species of the Galapagos Islands are greatly desired.

ECOLOGY AND DISTRIBUTION

The taxa of *Tiquilia* are all xerophytic perennials. Most species are woody, and some are subshrubs; one species is a small erect shrub. It is important to note, however, that some species can flower and fruit in their first year, thus functioning as annuals if eliminated by subsequent adverse conditions. Such plants have the obvious appearance of herbaceous annuals; some western North American species have, in fact, been erroneously reported to be herbaceous annuals.

Humphrey (1932) examined *Tiquilia canescens,* regarding its adaptations to dry conditions. He noted the following characteristics: (1) perennial root system capable of utilizing water, which may be available for only a few hours; (2) root system with horizontal and vertical roots, allowing absorption of water from light showers as well as the less transient moisture deeper in the soil; (3) pubescence; (4) revolute leaf blade margins; (5) stomata on abaxial leaf surface; (6) reduced number of stomata per unit area; (7) little intercellular space within the leaf; (8) leaf shedding during drought; (9) osmotic pressure above that of the average mesic leaf. Other species have not been examined, but *T. canescens* can be judged as, at least partially, representative of the genus.

The species are widely distributed over the xeric regions of North America and South America. The plants are usually dominants where they grow, but they usually do not grow in close proximity to other plants, with the exception of other species of the same genus. It is not uncommon to find two, three, or even four species growing together, especially in North America. In spite of this sympatry, no hybrids have been detected.

Subg. *Eddya* includes taxa of southwestern United States and north-central and northeastern Mexico. Subg. *Tiquilia* includes taxa of western United States and Mexico, and South America. Subg. *Eddya* is distributed principally in trans-Pecos Texas, Chi-

huahua, and Coahuila, but extends south to Hidalgo, east to Tamaulipas, and north and west to central Utah and southeastern Nevada. The taxa in this subgenus are primarily adapted to gypseous ($CaSO_4$) soils. Some taxa are gypsum endemics, while others are occasionally found growing in non-gypseous soils.

Tiquilia canescens diverges from the general pattern found in subg. *Eddya* by growing in various soil types, although it is most abundant in gypseous areas. Also, it is occasionally seen growing in close proximity with other plants. With these liberations it has been able to extend its range as far west as eastern California and into Baja California.

In five species of subg. *Eddya*, viz. *Tiquilia latior*, *T. hispidissima*, *T. tuberculata*, *T. turneri*, and *T. gossypina*, there is a reduction of the inflorescence to usually one flower; a reduction in overall leaf size (excepting *T. latior*); and a pronounced decrease in leaf blade width, partially due to an increased inrolling of the margin. The leaf reductions could be an adaptation enabling the leaves to live over a longer period of drought and therefore be available to function throughout the year as sporadic showers give moisture. With few flowers being produced, a plant's resources can be concentrated to producing a small number of fruits before drought again terminates the plant's activities. An added advantage is that during a prolonged period of rain the plants flower and fruit continuously, as long as moisture is available. *Tiquilia latior* was not observed in the field; however the other species were observed at various times of the year, and they consistently bloom after rains.

In subg. *Tiquilia*, sect. *Tiquiliopsis* comprises four species limited in distribution to the western United States and Mexico, and western Argentina. *Tiquilia cuspidata* grows mainly in southern Baja California and adjacent Sonora; it is replaced by *T. palmeri* from northern Baja California to southern California and western Arizona, with only a short band of sympatry. Again with only a short band of sympatry, *T. nuttallii* continues from southern California northward to Washington, and eastward into Utah, Arizona, and western Wyoming. This species also grows in western Argentina. Unlike the other South American species, it appears to be a recent introduction. *Tiquilia plicata* is sympatric with *T. palmeri*, less so with *T. nuttallii* in southern California, and grows also in Arizona.

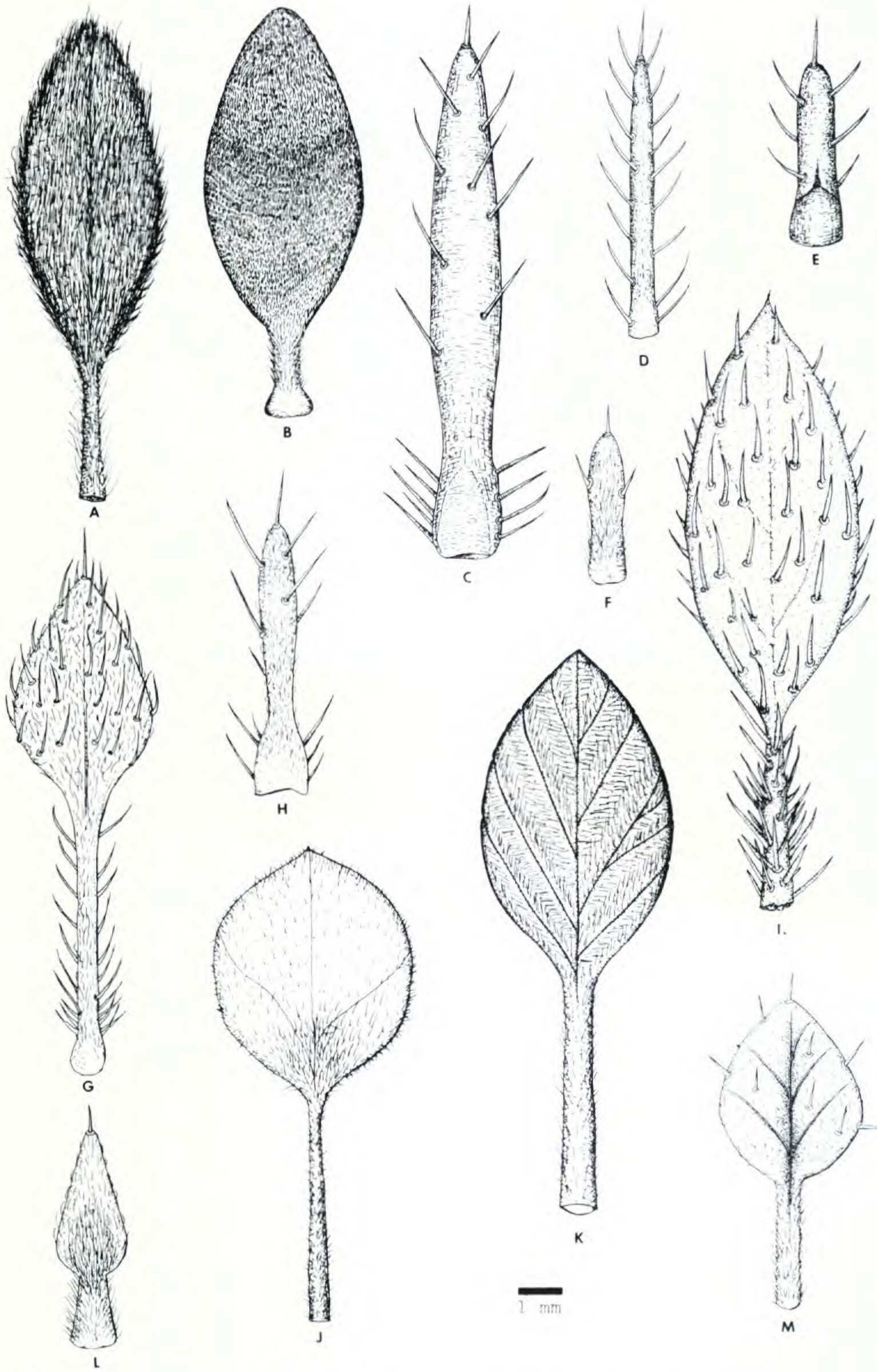

Figure 6. Drawings of leaves of *Tiquilia*. A, *T. canescens;* B, *T. greggii;* C, *T. latior;* D, *T. hispidissima;* E, *T. tuberculata;* F, *T. turneri;* G, *T. mexicana;* H, *T. gossypina;* I, *T. purpusii;* J, *T. nuttallii;* K, *T. plicata;* L, *T. cuspidata;* M, *T. palmeri.*

The species of this section grow in sand or a mixture of sand, clay, and gravel. They grow in a region with well-defined seasons of drought and rain. They have larger, broader leaves than most members of subg. *Eddya,* and differ also in producing inflorescences with clustered flowers, making them well-adapted to producing large quantities of seeds during the wet season and going dormant the remainder of the year.

The remaining three sections of subg. *Tiquilia* occur in western South America, including the Galapagos Islands. Three species, *Tiquilia atacamensis, T. elongata,* and *T. grandiflora,* have adapted to inland medium altitudes; the remainder are coastal.

The mainland species range from central Ecuador through Peru to the vicinity of Caldera and Copiapó in northern Chile. Seven species are endemic to Peru, six of them in the southern portion. One species is endemic to northern Chile; two species occur in southern Peru and northern Chile; and one species, *Tiquilia paronychioides,* occupies the total mainland distributional range of the genus. It is the most versatile South American species, even growing in close proximity to other plants in Ecuador. The three Galapagoan species are abundant on the islands, constituting a major part of the coastal flora (pers. comm., Dr. Aura Star, Oct., 1974; Wiggins & Porter, 1971).

It is not clear what ecological factors limit the distribution of the species, excepting the higher altitudes of the inland species. This factor was also observed by Johnston (1956). Essentially, all the species grow without competition in sand, which is abundant throughout the coastal and inland habitats. Species of different sections often grow together, but intrasectional sympatry is not great.

Of particular interest to South American phyto-geography is the lomas formation (Weberbauer, 1936), occurring principally in Peru and extending into northern Chile. The lomas vegetation, which receives moisture from winter and spring fogs, includes xerophytic, mesophytic, and even hydrophytic plants such as ferns, mosses, peperomias, and begonias where otherwise there would be only xeric plants, or none. The plant communities found in a lomas formation vary depending on altitude and distance from the sea, since the fogs are carried inland at consistent altitudes by the prevailing south and west winds (Weberbauer, 1936).

Tiquilia has adapted to receiving moisture from fog, and has often been collected in the lomas. I have seen populations in full bloom flourishing in locales where the inhabitants reported no rains had fallen for several months.

PHYLOGENY

Since there are no genera known to be closely related to *Tiquilia* in the New World, and no fossil evidence is reported, a hypothesized phylogeny must be inferred from present distributions, present relationships, and a knowledge of general geological and evolutionary trends. Present distributions have already been discussed.

There is no clear evidence as to whether the ancestral base chromosome number for the genus is $x = 9$ or $x = 8$. Both ascending and descending aneuploidy are known for other genera, although what appear to be descending series are more frequently encountered.

In order to express phylogenetic relationships graphically and numerically, the Wagner Divergence Index (Wagner, 1961) has been utilized. Characters have been assembled which can be valued 0.0 for primitive, 0.5 for intermediate, and 1.0 for derived. Designation of characters as primitive or derived is based on familiarity with the genus and generally accepted trends such as polyploidy or aneuploidy being derived characters and woodiness being a primitive character. The characters utilized are listed in Table 4. The divergence index values for the species are listed in Table 5. To conserve space, the characters are represented by their corresponding number in Table 4.

It must be understood that in a large genus such as *Tiquilia,* an overly complex set of values would be necessary for exact portrayal of inter-sectional and intra-sectional species relationships. To simplify matters, a few characters are weighted differently from section to section. For example, the character of open or closed nutlet scar: *T. hispidissima* of sect. *Eddya* is valued 0.0 as "open", while *T. ferreyrae* of sect. *Tiquilia,* with a wider scar, is valued 1.0 as "closed" in comparison with the other species in their respective sections. For purposes here, the base chromosome number for the genus is arbitrarily set at $x = 9$. When chromosome numbers are not known for a species, the number has been estimated, using exomorphic features as a primary guide.

Table 4. **Primitive and Derived Characters in Tiquilia.**

Primitive	Derived
1. Woody.	1. Herbaceous.
2. Leaves large and/or broad.	2. Leaves small and/or narrow.
3. Calyx not specialized.	3. Calyx indurated, plumose, or otherwise specialized.
4. Flowers in clusters.	4. Flowers solitary.
5. Corolla without appendages.	5. Corolla appendaged.
6. Stamens exserted.	6. Stamens included.
7. Style attachment apical.	7. Style attachment basal.
8. Nutlets 4 per fruit.	8. Nutlets consistently 2, or 1 per fruit.
9. Nutlets large, not spheroid.	9. Nutlets small, or spheroid.
10. Ornaments on nutlets small or absent.	10. Ornaments on nutlets large, or specialized extensions present on nutlet.
11. Nutlet scar broad.	11. Nutlet scar closed.
12. Diploidy.	12. Polyploidy.
13. Euploidy.	13. Aneuploidy.

Figure 5 is a diagram showing species relationships and degrees of advancement as calculated from the advancement index values in Table 5. The species are positioned according to their representative sections; the base of each line indicates the origin of the species it subtends.

It can be seen that the monotypic sect. *Stegnocarpus* has the most primitive characters. Because of this position, its flavonoid chromatograph pattern, unique for the genus, and its spheroidal fruit, which is approached only by species in sect. *Tiquilia*, *T. canescens* is judged to have diverged early in the history of the genus.

Sect. *Ptilocalyx*, another monotypic section, is judged to have diverged much later than sect. *Stegnocarpus*. Curiously, although inflorescence, fruit characters, and plant habit are unique in the subgenus, the leaves of *Tiquilia greggii* are essentially identical with those of *T. canescens* (sect. *Stegnocarpus*), and there is a strong similarity to those of *T. mexicana* (sect. *Eddya*). The globose inflorescence is interpreted as homologous with the inflorescence most common in subg. *Tiquilia*. *Tiquilia greggii* is the only species in subg. *Eddya* to demonstrate this affinity with subg. *Tiquilia*.

Table 5. **Divergence Index Values of the Species of Tiquilia.***

	1	2	3	4	5	6	7	8	9	10	11	12	13	Total
T. canescens	0.5	0.5	0.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0
T. greggii	0.0	0.5	1.0	0.0	1.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	4.5
T. latior	0.5	1.0	0.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.5
T. hispidissima	0.5	1.0	0.0	1.0	0.0	1.0	0.0	0.0	1.0	1.0	0.0	0.0	0.0	5.5
T. tuberculata	0.0	1.0	0.0	1.0	0.0	1.0	0.0	0.0	1.0	1.0	1.0	0.0	0.0	6.0
T. turneri	0.0	1.0	0.0	1.0	1.0	1.0	0.0	0.5	1.0	0.0	1.0	0.0	0.0	6.5
T. mexicana	1.0	0.5	0.0	0.5	0.5	1.0	0.0	0.5	1.0	1.0	1.0	0.0	0.0	7.0
T. gossypina	0.5	1.0	0.0	1.0	1.0	1.0	0.0	0.0	1.0	1.0	1.0	0.0	0.0	7.5
T. purpusii	1.0	0.5	0.0	0.5	0.5	1.0	0.0	0.0	1.0	1.0	1.0	0.0	0.0	6.5
T. nuttallii	0.5	0.5	0.0	0.0	1.0	1.0	0.5	0.0	1.0	0.0	1.0	0.0	1.0	6.5
T. plicata	0.5	0.0	0.0	0.0	1.0	1.0	1.0	0.0	1.0	0.0	1.0	0.0	1.0	6.5
T. palmeri	0.5	0.0	0.0	0.0	1.0	1.0	1.0	0.0	1.0	0.0	1.0	0.0	1.0	6.5
T. cuspidata	0.5	1.0	0.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	1.0	0.0	1.0	8.5
T. dichotoma	0.5	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0	3.5
T. simulans	0.5	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0	3.5
T. grandiflora	0.5	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	1.0	0.0	1.0	0.0	3.5
T. ferreyrae	0.5	0.0	1.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	1.0	1.0	0.0	4.0
T. atacamensis	0.5	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	3.5
T. tacnensis	0.5	1.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	1.0	1.0	0.0	4.5
T. elongata	0.5	0.0	0.0	0.0	1.0	1.0	0.0	0.0	1.0	0.0	1.0	1.0	0.0	5.5
T. hunteri	0.0	1.0	0.0	0.0	1.0	1.0	0.0	0.0	1.0	0.0	1.0	1.0	1.0	7.0
T. litoralis	0.5	0.5	0.0	0.0	0.5	0.5	0.0	0.0	1.0	0.0	1.0	1.0	1.0	6.0
T. conspicua	0.5	0.0	0.0	0.0	1.0	0.5	1.0	0.0	1.0	0.0	1.0	1.0	0.0	6.0
T. paronychioides	0.5	1.0	0.0	0.0	0.0	1.0	0.5	0.0	1.0	0.0	1.0	1.0	0.0	6.0
T. nesiotica	0.5	1.0	1.0	0.5	0.0	1.0	0.0	0.0	1.0	0.0	1.0	1.0	0.0	7.0
T. galapagoa	0.5	1.0	1.0	0.5	0.0	1.0	0.0	0.0	1.0	0.0	1.0	1.0	0.0	7.0
T. darwinii	0.5	1.0	1.0	0.5	1.0	0.5	0.0	0.0	1.0	0.0	1.0	1.0	0.0	7.5

*Utilized characters are represented by numbers corresponding with the characters in Table 4.

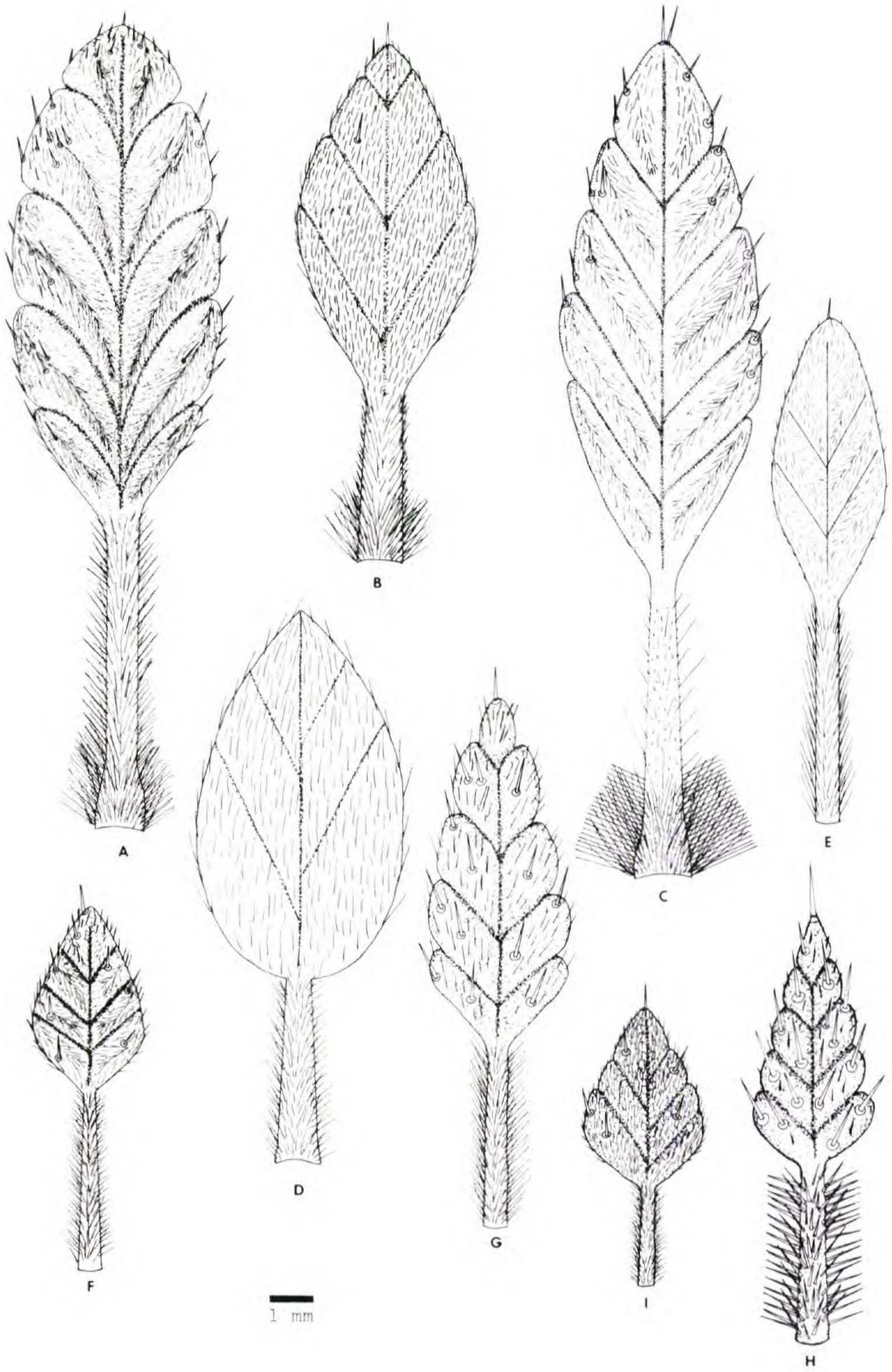

Figure 7. Drawings of leaves of *Tiquilia*. A, *T. dichotoma*; B, *T. simulans*; C, *T. grandiflora*; D, *T. ferreyrae*; E, *T. atacamensis*; F, *T. tacnensis*; G, *T. elongata*; H, *T. hunteri*; I, *T. litoralis*.

Sect. *Eddya* is dominated by a trend toward ovoid nutlets with a closed attachment scar and large ornaments. Fabre (1966) has noted a definite trend in the Boraginaceae for xeric plants to have rougher nutlets, and mesophytes to have smoother nutlets. There is also a trend toward a linear or lanceolate leaf blade, and generally reduced leaf size, the petiole often being extremely reduced and scale-like. *Tiquilia mexicana* follows this second trend only slightly, and *T. purpusii* not at all.

Tiquilia latior, the most primitive species of the section, has followed these general trends, but to a lesser degree than other species. Of special note is the obpyriform or rarely ovoid shaped nutlet with small ornaments and an attachment scar much narrower than in *T. greggii* but broader than those of any other species in its section. Also noteworthy is the geographic distribution of the species, viz. along the Colorado and Little Colorado River basins in Arizona, Nevada, and Utah, near the proposed center of origin of the genus (see below). The nutlets of the closely related species, *T. hispidissima,* have a slightly narrower attachment scar. This species grows farther east and south, in New Mexico, trans-Pecos Texas, and adjacent Mexico.

Tiquilia cuspidata of sect. *Tiquiliopsis* is the most derived species of the genus and is in a section containing well-advanced species. The section is characterized by a base chromosome number of $x = 8$; a trend from sub-apical to gynobasic style attachment; variety in nutlet shape; and innovations, such as the development of underground rhizomes (*T. plicata*), and loss of mericarps and resulting reduction of nutlets per fruit (*T. cuspidata*).

The tetraploids of sect. *Tiquilia* (where $n = 16$) seem to have an unusual concentration of primitive characters. This fact might possibly be attributed to polyploid buffering (Stebbins, 1971). Stebbins (1966) has noted that taxa with low chromosome numbers tend to undergo more differentiation than do taxa with high chromosome numbers.

The ovoid shaped fruit, usually of two nutlets, is of particular note in taxa of sect. *Tiquilia,* and the hemi-ovoid nutlets have broad, flattened, ventral surfaces. The pericarp covers only the convex surface, reminiscent of *Tiquilia canescens* of sect. *Stegnocarpus.* Since the pericarp character is lost in all North American species, excepting *T. canescens,* it is inferred that the movement of the ancestral stock into South America must have occurred at an

early point in the evolution of the genus. Doubling of the chromosome complement likely took place early in the development of the South American species, since there are no known diploids. A direct introduction of tetraploids from North America is possible, but no North American tetraploids have been found.

There is a definite trend toward inrolling of the pericarp. There is none in *Tiquilia dichotoma; T. simulans* has a slight inrolling; and *T. ferreyrae* has a more pronounced inrolling, the flattened ventral surface becoming correspondingly smaller. The stamens are consistently exserted in all species.

Sect. *Sphaerocarya* appears to be directly derived from advanced stock of sect. *Tiquilia*. Among the species of sect. *Sphaerocarya* there is a gradual shortening of the stamens from an exserted position to an intermediate and finally to an included position. There is also a continuation of the trend toward inrolling of the pericarp, and development of a spheroidal nutlet, culminating in *Tiquilia conspicua* with spheroidal nutlets and a gynobasic style; *T. litoralis* with spheroidal nutlets and reduction of chromosome number to $n = 15$; and *T. hunteri* with reduced spheroidal nutlets and chromosome number $n = 14$. Other species which have been counted are tetraploids, $n = 16$.

The species of sect. *Galapagoa* are characterized by ovoid, black nutlets, a loss of corolla color, and a reduction in size of all organs. Definite chromosome counts have not been obtained, but an approximate count (n = ca. 14–16) for *Tiquilia paronychioides*, the only mainland species, suggests polyploidy.

The relations of the species of sect. *Galapagoa* with other South American species are not clear, as indicated by a broken line in Figure 5. The nutlet characters are unlike those of any other species on that continent. Similarities between nutlets of *Tiquilia paronychioides* (sect. *Galapagoa*) and *T. cuspidata* (sect. *Tiquiliopsis*) suggest the possibility of a second introduction from North America. However, on the basis of morphological and chromosomal evidence it seems better to assume a closer relationship with the other South American sections and to attribute the similar nutlet characters to convergence in similar habitats. Additional chemical studies would provide useful evidence for determining these relationships.

Ancestral *Tiquilia* was presumably a member of the Madro-Tertiary Geoflora which, according to Axelrod (1958), apparently

was derived from the Neotropical Tertiary Geoflora. Johnson (1968) includes *Coldenia* (sensu lato) with plants showing relationships with southern and western elements rather than with northern elements. Rzedowski's (1973) conclusions also support the hypothesis of a Neotropical origin of *Tiquilia*. The subfam. Ehretioideae is, of course, typically of tropical or warm temperate affinities.

It is impossible to fix accurately the time and place of origin of *Tiquilia*. There is no fossil record. However, the history of the genus probably began in western North America. The trend toward aridity beginning in Eocene and Oligocene times gave a selective advantage to, and allowed the spread of, semi-xeric plants previously limited to scattered xeric pockets. The generally xeric conditions of the succeeding Miocene time probably favored the establishment and radiation of *Tiquilia*.

The two subgenera, after or concomitant with spatial separation, were further separated by differences in chromosome numbers and ecological adaptations. The divergence occurred at an early point in the evolution of the genus, as evidenced by the primitive morphological characters, previously discussed, in the South American sect. *Tiquilia*.

Subg. *Eddya* ($x = 9$), developing a tolerance for infertile gypseous soils, was able to move into the relatively open habitats in gypseous areas toward the east, particularly in New Mexico and eastward and southward into Texas and Mexico. Speciation was enhanced by edaphic conditions, with fertile soils interrupting gypseous areas and providing effective barriers between populations that might otherwise be continuous (see Grant, 1963, p. 456; 1971, p. 114). Continuing orogeny in the late Pliocene and Pleistocene times brought more extreme xeric conditions and inhibited further migration.

Subg. *Tiquilia* ($x = 8$) was limited to the western part of the continent, migration being mostly northward and southward. Edaphic adaptations were toward "pure" sand, or sandy soils. Sect. *Tiquiliopsis* was established in western North America. The four extant species are well differentiated and distinct.

A segment of the stock moved into South America, possibly by long-distance dispersal, or by a series of shorter steps along dry coastal pockets. Speciation was probably enhanced by topography and edaphic conditions, with frequent habitat interruptions by

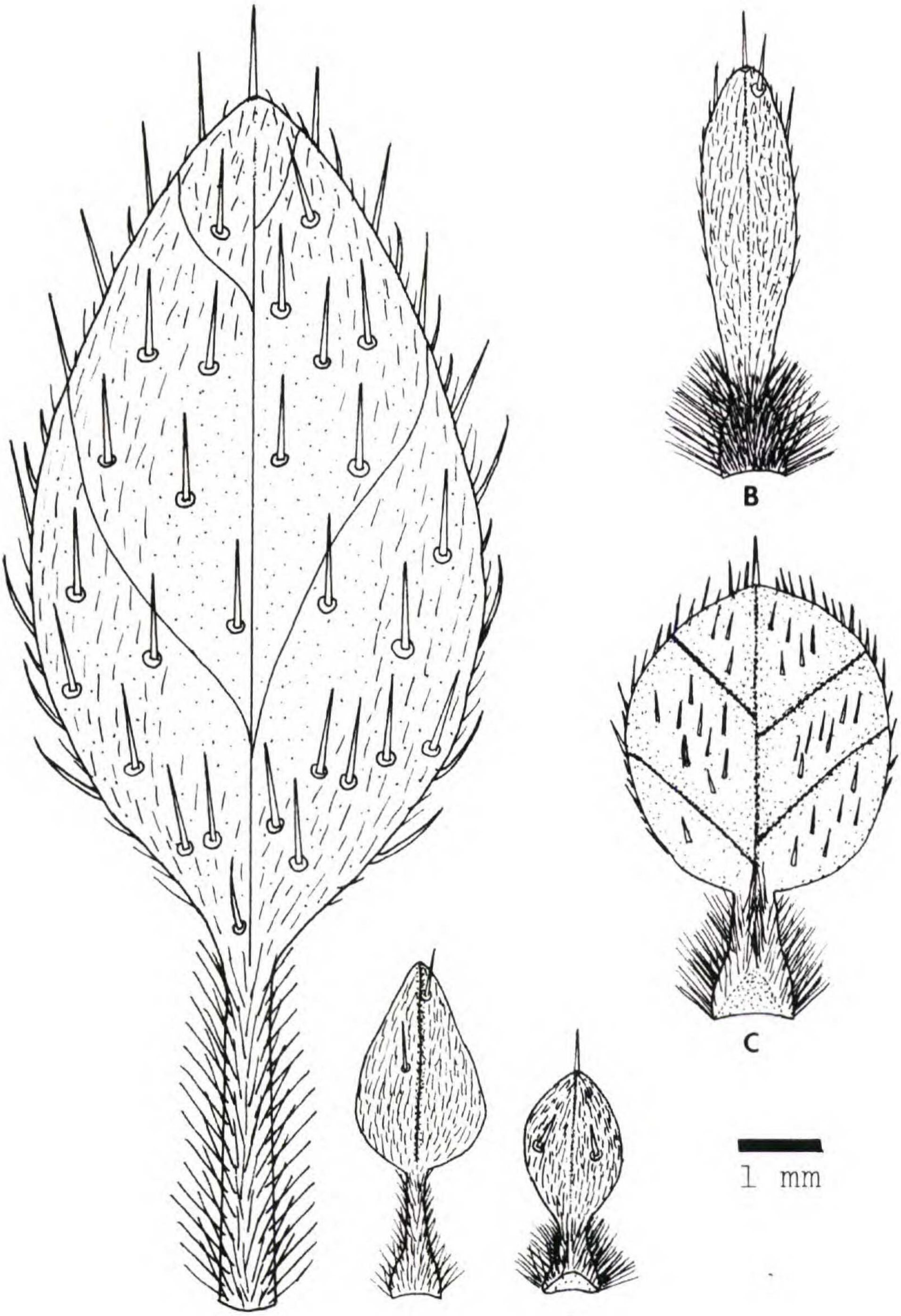

Figure 8. Drawings of leaves of *Tiquilia*. A, *T. conspicua;* B, *T. paronychioides;* C, *T. galapagoa;* D, *T. nesiotica;* E, *T. darwinii.*

mountains and fertile river valleys. The center of variation is southern Peru.

DISPERSAL OF DISJUNCT TAXA

The subject of amphitropical disjuncts has been discussed by Bray (1900), Johnston (1940), and others (Constance, 1963; Grant, 1959; Heckard, 1963; Raven, 1963), and more recently by Hunziker (1972), Raven (1972, 1974), Turner (1972), and Werger (1973). Hunziker *et al.* (1972) interpreted their data on *Larrea* as indicating a South American origin of the genus and a later introduction into North America. However, Turner (1972) and Porter (1974) visualized the reverse as equally possible. Sanderson (1975) used chemical, morphological, and cytological data to show that North American *Hymenoxys odorata* and *H. anthemoides* were not as closely related as their morphology seemed to suggest. Following Turner (1972), he classified them as allojuncts. Payne *et al.* (1973), using sesquiterpene lactone chemistry, found that the North American and Chilean populations of *Ambrosia chamissonis* represent one variable species presumably derived from extant North American populations; accordingly, they are autojuncts (Turner, 1972).

Cytological and morphological data indicate that all the South American species of *Tiquilia* in sects. *Tiquilia, Sphaerocarya,* and *Galapagoa,* being derived from extinct North American stock, are allojuncts. However, populations of *T. nuttallii* (sect. *Tiquiliopsis*), occurring in the northwestern United States and northwestern Argentina have apparently identical morphology and flavonoid chromatograph patterns. Unfortunately, chromosome counts have not been obtained from any South American populations of this species. In the absence of conflicting data, the South American populations of *T. nuttallii* are considered autojuncts.

Three explanations have been offered for the presence of transtropical disjunct, closely related taxa on the two continents: (1) an old American desert was shared, and continuous with both continents, (2) migration took place by a series of steps through isolated hospitable habitats, or (3) by one or few long jumps (long distance dispersal).

The first explanation has been rejected for the following reasons: (1) there was no continuous land connection between North Amer-

ica and South America until about the Pliocene (Raven & Axelrod, 1974); (2) relatively few plants, and no vertebrates, have been exchanged (Raven, 1963); (3) the tropical forest has always occupied the central area within the tropics (Grant, 1959); and (4) fossil evidence indicates that floras of North and South America were separated and developed independently during Paleozoic and Mesozoic times (Constance, 1963).

The remaining two explanations seem highly unlikely; however, the plants are there and they must have arrived by one of these methods. As stated by Grant (1959), the two methods are not mutually exclusive.

Although desert vegetation did not reach its present aspect until Pliocene time (Johnson, 1968), desert areas were probably present at least by Miocene time (Turner, 1972). Although there was no continuous Central American land bridge, recent opinions are that throughout Tertiary time there were shifting groups of islands and peninsulas attached at different times to one continent or the other (Bartlett & Barghoorn, 1973). This unstable condition would no doubt present a series of open habitats by which *Tiquilia* could have crossed to the South American mainland. The large primitive fruit was probably buoyant (as is that of *T. canescens*) and could have been transferred from island to island by drift, rafting, or by birds. *Tiquilia* in Central America could have been eliminated after subsequent stabilization of the land and introduction of more competitive plants.

The feasibility of long-distance dispersal by birds has been discussed with both negative and affirmative opinions. Cruden (1966) discarded the possibility of external transport because propagules would be unlikely to remain attached after repeated preenings and exposure to the elements during the time (one month) that he estimated would be required for the trip. He believed internal transport was impossible because seed passage takes only a few hours. He further questioned whether the amount of genetic variability transported in one or a few seeds would be sufficient to account for the morphological variation exhibited by various taxa.

Carlquist (1967, 1974), on the other hand, believes many introductions to remote islands were made by birds. Grant (1959) affirmed the plausibility of birds as vectors of long-distance dispersal between North and South America. He noted that all of the twelve herbaceous species of the Polemoniaceae in South America have

mucilaginous seeds, although, in some cases, this feature represents an exceptional condition for the genus or section.

Tiquilia has no adaptations for long-distance dispersal on the external anatomy of birds, and there is no indication that the ancestral stock had any. The taxa occur in sandy rather than muddy habitats, and their fruits are not mucilaginous or spiny. The closely related *Coldenia procumbens* sometimes produces fruits with some spinelike processes; however, the processes are broad and blunt and, in the opinion of this investigator, would not cause the fruits to adhere to a bird.

The remaining possibility is internal transport. *Tiquilia* fruits are inconspicuous and dry and therefore do not seem particularly adapted for dispersal by birds. However, many of the migratory shore birds eat various types of plant material. *If* the nutlets could remain in the bird's gut, undamaged, until arrival at a suitable habitat, then there is reason to consider the possibility of birds as agents of long-distance dispersal of *Tiquilia.*

The calculated age of the Galapagos Islands, about one million years, limits the time of migration to the islands and subsequent evolution of the three Galapagoan species to the same time period. Nutlets were transported from the South American mainland to the islands possibly by oceanic drift, rafting, or by birds. Carlquist (1967), in analyzing the flora of the Galapagos Islands, believed many introductions were made by oceanic drift as well as by birds. The nutlets of the species in this section do not float, but could have been transported with portions of the plant or on other buoyant material. Previous adaptation to dry, sandy habitats would facilitate establishment on a beach and subsequent inter-island dispersal, once the islands were reached. However, it is not known whether the seeds would survive long periods of immersion in salt water.

There being no spines or viscid material on the nutlets, they would have to be carried internally if birds are the vectors. There are, however, no data concerning feeding habits of birds on *Tiquilia.*

TAXONOMIC TREATMENT

Tiquilia Persoon, Syn. Pl. **1:** 157. 1805.

Monomesia Raf., Flora Telluriana **4:** 87. 1836, *nomen. superfl.*, based on an unnamed specimen collected by Dombey (*Dombey 364*), probable duplicate GH!), described in passing by Jussieu, Gen. Pl. 130. 1789, as a possible con-

gener of *Coldenia*.
Galapagoa Hook. f., Trans. Linn. Soc. **20:** 196, 197. 1847.
Stegnocarpus Torrey & Gray, Senate Executive Doc. No. 78, 33rd Congr., 2nd Sess. **2:** 169. *Pl. 7.* 1857.
Eddya Torrey & Gray, *Ibid.:* 170. *Pl. 9.* 1857.
Ptilocalyx Torrey & Gray, *Ibid.:* 170. *Pl. 8.* 1857.

Pseudo-dichotomously branching perennials often flowering the first year, fruticose or suffrutescent (bark, when present, usually exfoliating) or herbaceous, prostrate, spreading or bushy-branched; pubescence variable. Leaves solitary at the nodes or in clusters on short branches, stem apices, or the nodes; blades green to grey, linear to lanceolate, ovate, obovate, or suborbicular, 2.5–23.0 mm. long, margins revolute, entire or crenate, the lateral veins running to the sinuses when crenate; petioles subrectangular to ovate-trullate or filiform, or a combination of both. Flowers sessile, solitary or few and axillary, or in clusters usually subtended by bracts. Calyces 5-lobed, the lobes triangular to lanceolate, narrowly ovate, or subulate. Corollas white to pale lavender to deep blue or purple, often with a yellow throat; deciduous in North America, deciduous or persistent in South America, funnelform, occasionally cylindrical; lobes 5, rounded, imbricate in bud. Stamens 5, included in North America, included or exserted in South America, equal or unequal, adnate to the corolla tubes usually at 3 levels, sometimes equally, level of insertion variable. Styles cleft once, the stigmas capitate; attachment to nutlets apical, sub-apical, sub-basal, or basal. Nutlets 1–4. Cotyledons (after germination) elliptic or hippocrepiform. Base chromosome numbers, $x = 9$, $x = 8$; derived chromosome numbers, $n = 16, 15, 14$. TYPE SPECIES: *Tiquilia dichotoma* (Ruiz & Pavon) Persoon.

The name for the genus was taken from the vernacular name of the type species, *Tiquil-tiquil.* The vernacular name is probably a derivative of the Quechua word *t'ika,* meaning flower.

Tiquilia consists of two subgenera. One subgenus comprises three sections, and the other, four. The subgenera and the sections can be distinguished by the following key.

KEY TO THE SUBGENERA & SECTIONS OF TIQUILIA

a. Nutlet ovoid to obpyriform, with collicula or tubercula 0.05 mm. across or larger; or if ornaments are smaller or absent, the nutlets 0.8 mm. or longer, and the petiole elliptic-rectangular, or the nutlet pubescent apically, or the fruit

spheroid, of 4 nutlets. Style attachment apical. North America: United States and Mexico. ..... 1. *Tiquilia* subg. *Eddya* (page 505, species 1–9).
b. Fruit lobed, not spheroid. ..... c.
c. Plant procumbent, herbaceous from a woody caudex or if shrubby, not erect; nutlet not pubescent, not retained in a plumose calyx. ..... 1c. *Tiquilia* sect. *Eddya* (page 514, species 3–9).
c. Plant an erect shrub, fruit of 1 nutlet, pubescent apically, retained in a plumose calyx. ..... 1b. *Tiquilia* sect. *Ptilocalyx* (page 510, species 2).
b. Fruit not lobed, spheroid, of 4 nutlets. ..... 1a. *Tiquilia* sect. *Stegnocarpus* (page 506, species 1).
a. Nutlet ovoid to spheroid, minutely colliculate, minutely aculeate, granular (in all cases, the ornaments smaller than 0.04 mm. across), or smooth. Style attachment apical, sub-apical, sub-basal, or basal. North and South America. ..... 2. *Tiquilia* subg. *Tiquilia* (page 530).
d. Nutlet not hemi-ovoid, ventral surface not broadly flattened; corolla deciduous; stamens included or slightly exserted. ..... e.
e. Nutlet ovoid, without the corresponding characters of sect. *Sphaerocarya;* or spheroid, smooth or minutely aculeate with a gynobasic style. ..... f.
f. Nutlet ovoid, the attachment scar running almost the full length, terminating more or less equidistant from apex and base; style attachment apical or sub-apical; petiole ovate-trullate. South America. ..... 2d. *Tiquilia* sect. *Galapagoa* (page 560, species 24–27).
f. Nutlet spheroid or ovoid; style attachment sub-apical, sub-basal, or basal; petiole filiform, or if trullate then the nutlet attachment scar beginning near the base running more or less ¾ the length, and style attachment basal. North and South America. ..... 2a. *Tiquilia* sect. *Tiquiliopsis* (page 530, species 10–13).
e. Nutlet spheroid (exclude if style is gynobasic and nutlets are without a basal plug and either smooth or minutely aculeate), or ovoid in ventral view, elliptical and beaked in lateral view, mottled grey, brown, and black. South America. . 2c. *Tiquilia* sect. *Sphaerocarya* (page 550, species 18–23).
d. Nutlet hemi-ovoid, ventral surface broadly flattened, corolla persistent, stamens greatly exserted, 3.0–8.0 mm. South America. ..... 2b. *Tiquilia* sect. *Tiquilia* (page 542, species 14–17).

Tiquilia subg. **Eddya** A. Richardson. TYPE SPECIES: *Tiquilia hispidissima* (Torrey & Gray) A. Richardson.

Leaf margins entire. Nutlets ovate to obpyriform, with colliculа or tubercula 0.05 mm. across or larger; or if ornaments are smaller or absent, the nutlets 0.8 mm. or longer, and the petioles elliptical-rectangular, or the nutlets pubescent apically, or the fruit spheroid, of 4 nutlets. Stamens unequal, included, adnate to the corolla tubes at 3 levels. Style attachments apical. Cotyledons (after germination) elliptical. Chromosome number, $n = 9$ (one species aneuploid with $n = 8$).

Tiquilia sect. **Stegnocarpus** DC., Prodr. Syst. Nat. **9:** 559. 1845.

TYPE SPECIES: *Tiquilia canescens* (DC.) A. Richardson.

Herbaceous to suffrutescent. Leaves solitary at the nodes and in clusters on short branches or the stem apices; blades ovate, lanceolate, or obovate. Flowers axillary, solitary, occasionally 2 or 3. Calyces persistent. Fruits spheroidal. Chromosome number, $n = 9$.

The single species in this section is the most widespread of the genus, found in the United States and Mexico from the Texas gulf coast to the Pacific coast.

1. **Tiquilia canescens** (DC.) A. Richardson, Sida **6:** 236. 1976.

Synonymy and typification are cited under the varietal headings.

Herbaceous to suffrutescent, procumbent or spreading, 1.0–3.0 dm. high, with one report of a shrub to 6.0 dm. high, forming mounds or mats to 6.0 dm. across from woody taproots; caudices to 2.0 cm. thick; younger branches villous with some thin stiff spreading hairs to 0.9 mm. long; short branches often appearing on alternating sides of the main stem, giving a zigzag effect. Leaves solitary, axillary, or in clusters on short branches; blades (Figure 6A) green to grey or nearly white, 7.0–11.5 mm. long, 4.0–8.5 mm. broad, ovate, lanceolate, or obovate, sometimes decurrent on the petiole, curling back markedly under dry conditions, otherwise fairly flat except for a tendency in western United States and Mexico for the leaves to roll slightly, giving convex upper surfaces, the blades appearing thicker; upper surfaces densely pubescent with short straight variously appressed hairs, overlaid with antrorsely appressed or inclined larger stiff bristles to 0.6 mm. long with thickened mineralized bases, these sometimes more prominent along the margins; lower surfaces more densely pubescent; petioles filiform, 1.5–7.0 mm. long, villous with dense spreading bristles to 0.9 mm. long. Calyces persistent, 3.0–5.0 mm. long, villous and densely covered by fine straight antrorsely inclined or appressed hairs to 0.9 mm. long on outer surfaces; lobes subulate, linear or triangular, slightly unequal, sometimes ciliate, with sparse antrorsely appressed hairs on inner surfaces, free 2/3 to 3/4 the length. Corollas opening in the morning and falling in the evening; white to pink, purple, or blue, often with a yellow throat, 3.5–9.0 mm. long, not appendaged; the bud glabrous or villulose. Stamens adnate to the corolla tubes ca. 1/4 the length from base to limb. Styles 2.0–3.5 mm. long, cleft 1/3 the

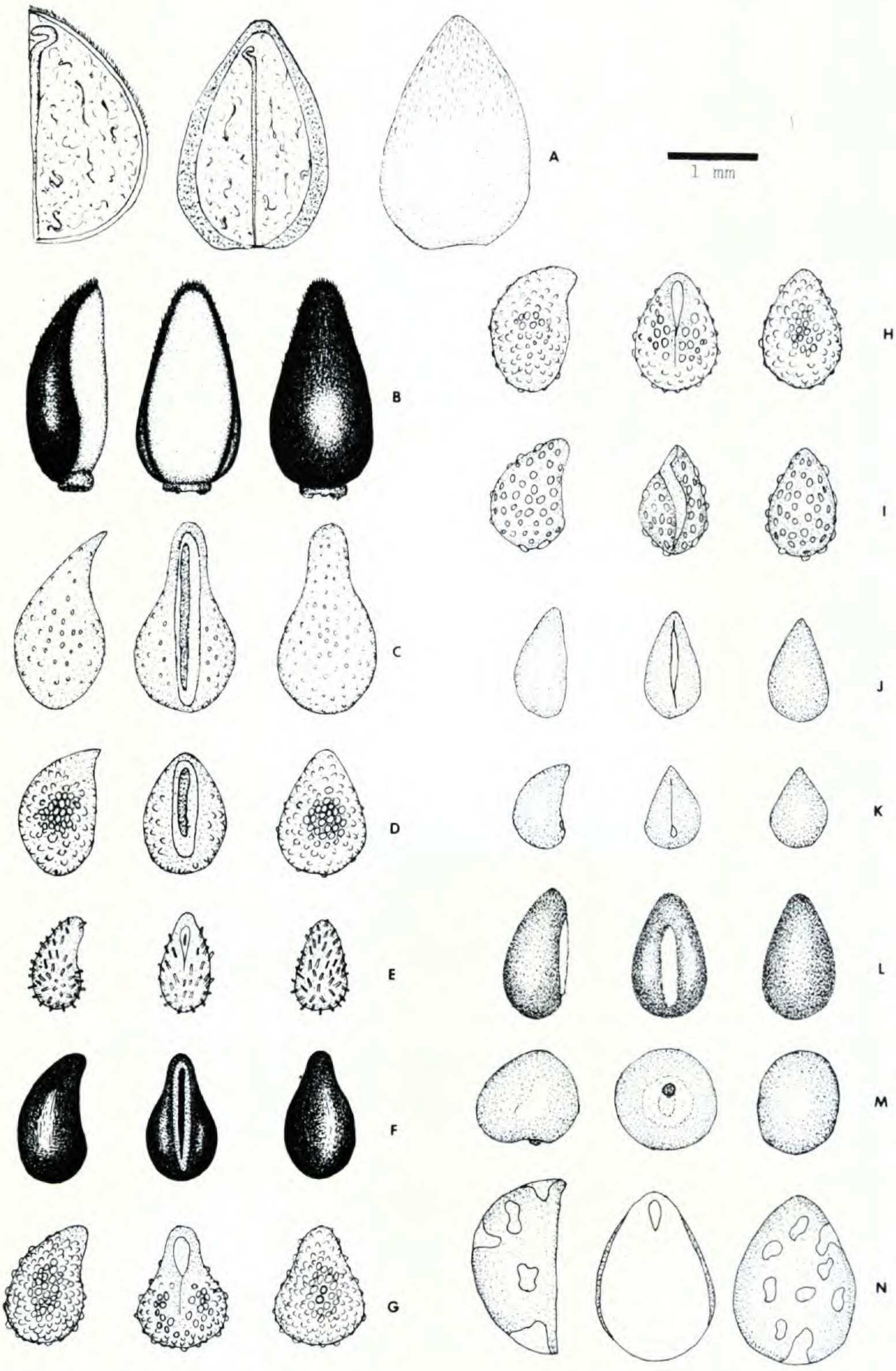

Figure 9. Drawings of nutlets of *Tiquilia*, left to right, lateral, ventral, and dorsal views. A, *T. canescens;* B, *T. greggii;* C, *T. latior;* D, *T. hispidissima;* E, *T. tuberculata;* F, *T. turneri;* G, *T. mexicana;* H, *T. gossypina;* I, *T. purpusii;* J, *T. nuttallii;* K, *T. plicata;* L, *T. cuspidata;* M, *T. palmeri;* N, *T. dichotoma.*

length, occasionally less; stigmas large, subbifurcate. Fruits spheroidal with 4 longitudinal grooves, 2.1–3.0 mm. across, 2.2–2.8 mm. high, exocarp thickened, smooth or minutely colliculate, shiny light brown to dull dark brown, glabrous or puberulent apically, sometimes over all with short, retrorsely appressed straight hairs; nutlets (Figure 9A) 1–4, usually 4.

Tiquilia canescens is often the dominant plant where it grows, but it also grows with such dominants as *T. greggii, T. hispidissima, Gutierrezia microcephala, Larrea, Leucophyllum, Pinus,* and *Yucca.* It also grows in association with *Acacia, Agave, Dasylirion, Fouquieria, Franseria, Prosopis, Nerisyrenia, Opuntia, Selinocarpus,* annuals, and grasses. It has been observed *in situ* with five other species of *Tiquilia: T. gossypina, T. greggii, T. hispidissima, T. mexicana,* and *T. purpusii,* and is geographically sympatric with *T. cuspidata, T. nuttallii, T. palmeri,* and *T. plicata.*

Two varieties are recognized. Their distributions are shown in Figure 11. They may be distinguished and characterized by the following key.

KEY TO THE VARIETIES OF TIQUILIA CANESCENS

Corolla 3.5–7.5 mm. long. ..... 1a. *T. canescens* var. *canescens.*
Corolla 7.0–9.0 mm. long. ..... 1b. *T. canescens* var. *pulchella.*

1a. **Tiquilia canescens** var. **canescens**

Coldenia canescens DC., Prodr. Syst. Nat. **9:** 559. 1845. TYPE: **Mexico:** Tamaulipas. Inter Santander (Jimenez) et Victoria, *Berlandier 2256.* (Holotype, G, not seen. Photograph TEX! Isotypes, GH! NY! US! Possible isotype, NY!).

Stegnocarpus canescens (DC.) Torr., *In* Torrey & Gray, Senate Executive Doc. No. 78, 33rd Congr., 2nd Sess. **2:** 169–170. *Pl. 7.* 1857.

Coldenia canescens var. *subnuda* I. M. Johnst., Proc. Calif. Acad. IV. **12:** 1137. 1924. TYPE: **Mexico:** BAJA CALIFORNIA. San Nicolas Bay, 16 May 1921, *I. M. Johnston 3731.* (Holotype, CAS! Isotypes, F! GH! NY! UC! US!).

DISTRIBUTION: *Tiquilia canescens* var. *canescens, n* = 9, is by far the most widespread taxon of the genus. It grows in Arizona; southeastern California; southern Nevada; southern New Mexico; in Texas from El Paso County eastward to Bexar County and from Kent County southward to Cameron County; in Mexico in Baja California; eastern Chihuahua; Coahuila; northwestern Hidalgo; Nuevo Leon; Querétaro; San Luis Potosí; Sonora; Tamaulipas; and eastern Zacatecas (Figure 11). It grows from the xeric extremes of

Baja California and the southeastern California deserts to the moderately xeric conditions of south Texas; from the moderate temperature ranges in the Mexican states of Hidalgo and Querétaro, well south of the Tropic of Cancer, to the harsher extremes of southern Nevada; at altitudes from 8 meters to 2530 meters; in gypseous or calcareous loam or clay, or in desert sands. It is the only North American taxon showing any consistent ability to compete with other plants, often growing with grasses and annuals, although more often growing in the absence of any competition.

As with the other taxa, flowering is controlled by moisture availability, the plants becoming dormant and dying back during extended dry periods. The plants flower January through December in Texas, but less in other localities.

Vernacular names are Oreja del Perro and Yerba del Pobre. In Mexico, a decoction of leaves and stems is used to bathe wounds (*Latorre 15* TEX). It is also used for sweat baths, and to prevent going to sleep after eating (*Lundell 5266* LL). Conflicting data on herbarium labels report no forage value (*JTC-Kav s.n.* GH), and good forage value (*Hershey 3415* GH). Personal observations in various conditions including areas where cattle and goats were grazing, indicate there is little or no forage value, since no grazing damage to plants has ever been seen. The only plant part damaged by insects is the corolla.

Johnston (1924) first differentiated *Coldenia canescens* var. *subnuda* on the basis of fruit pubescence. Later (1966) he found this character inconsistent, but he retained the variety on the basis of leaf size, color, and pubescence. There is no geographical correlation of those characters to justify a varietal status; rather there is a scattering throughout the distribution range, with plants having characters of the two "varieties" often in the same population.

1b. **Tiquilia canescens** var. **pulchella** (I. M. Johnston) A. Richardson, Sida **6:** 236. 1976.

Coldenia canescens var. *pulchella* I. M. Johnston, Jour. Arnold Arb. **20:** 379. 1939. TYPE: **Arizona:** YUMA CO. Kofa Mountains, 1700 ft., 24 Mar. 1933, *Shreve 6527.* (Holotype, GH! Isotypes, ARIZ! F!).

DISTRIBUTION: This variety is known only in extreme southwestern Arizona (Yuma Co., rarely Yavapai Co.), and southeastern California (Imperial Co., rarely Riverside Co.) in association

with *Fouquieria, Franseria, Larrea,* and *Parkinsonia.* It is almost completely isolated geographically from *Tiquilia canescens* var. *canescens* (Figure 11).

Johnston (1939) described *Coldenia canescens* var. *pulchella* based on geographic correlation of greater corolla length and limb diameter, and intense corolla color. In this investigation, the corollas were found to be somewhat smaller than reported by Johnston. He probably soaked them prior to measuring them since, upon wetting, they increase in length about the difference between his measurements and those of this investigator. It seems more practical and useful to use measurements of dried corollas. Herbarium label data show corolla color comparable to that of *T. canescens* var. *canescens.*

This variety flowers February through June; September, November, and December.

No chromosome counts have been reported.

Tiquilia sect. **Ptilocalyx** A. Richardson. TYPE SPECIES: *Tiquilia greggii* (Torrey & Gray) A. Richardson.

Erect shrubs to 1.0 meter tall. Leaves in axillary or terminal clusters. Flowers in terminal bracteate globose clusters. Calyces plumose, deciduous, retaining the fruits. Fruits single nutlets, 3 mericaps aborting, remaining on the ventral surfaces of the nutlets as a membranous tissue. Nutlets ovoid-obpyriform, apically puberulent with spreading and retrorsely appressed hairs. Chromosome number $n = 9$.

This monotypic section includes a species found in northern Mexico, southern New Mexico, and trans-Pecos Texas.

2. **Tiquilia greggii** (Torrey & Gray) A. Richardson, Sida **6:** 236. 1976.

Ptilocalyx greggii Torrey & Gray, Senate Executive Doc. No. 78, 33rd Congr., 2nd Sess. **2:** 170, 171. *Pl. 9.* 1857. TYPE: Common in New Mexico, May-October 1849, *Wright 492* (Holotype, GH! Isotypes, GH! NY! UC! US!).

Coldenia greggii (Torrey & Gray) Gray, Proc. Am. Acad. **5:** 340, 341. 1862.

Low erect shrubs to 1.0 meter tall, compact, branches numerous and crowded; base to 1.3 cm. diameter; young branches villous with occasional stiff bristles to 0.7 mm. long. Leaves (Figure 6B) cinereous, sometimes greenish; blades ovate or elliptic, 4.5–8.5 mm. long, 2.1–4.2 mm. broad; upper surfaces covered densely with short

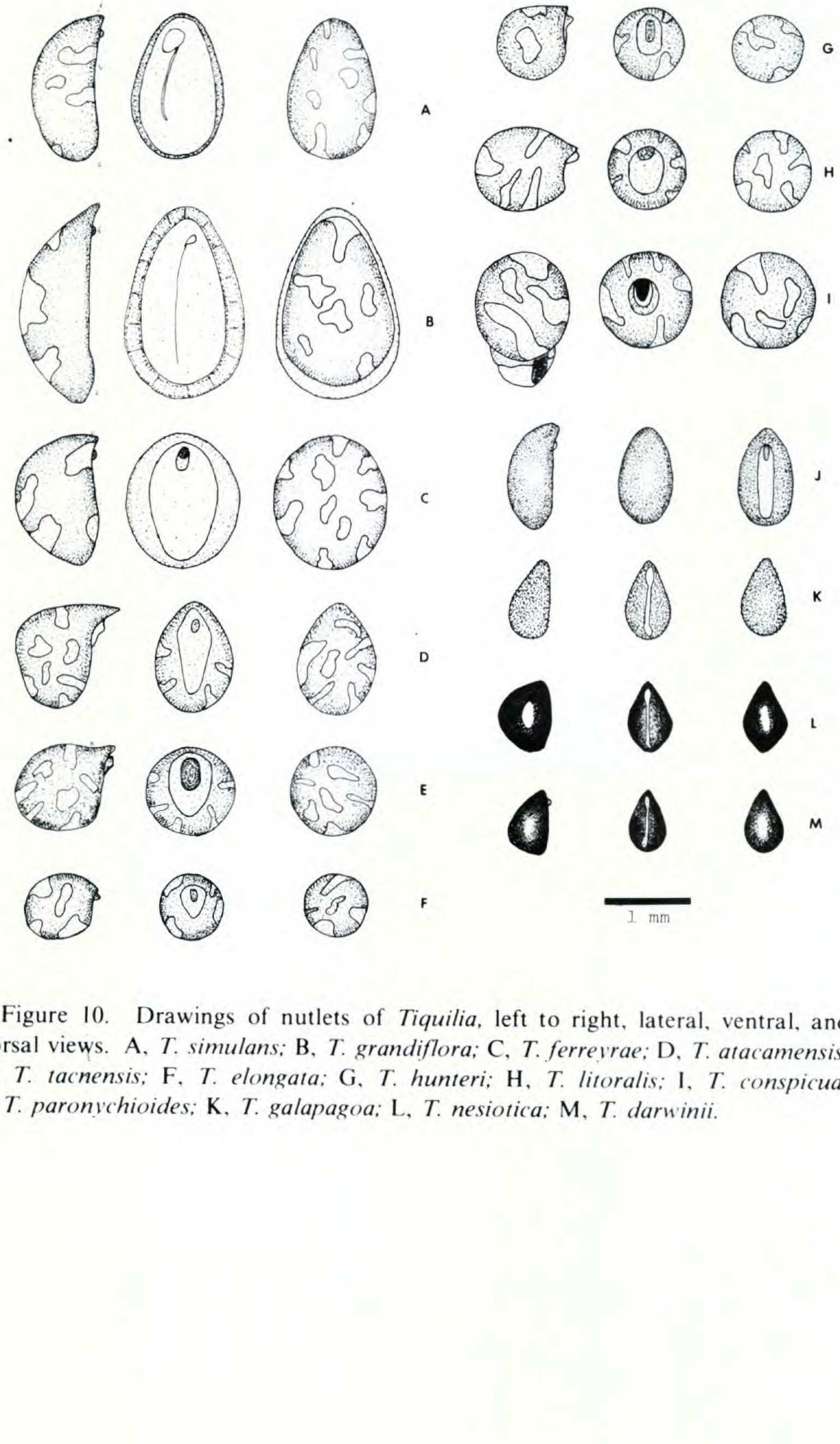

Figure 10. Drawings of nutlets of *Tiquilia,* left to right, lateral, ventral, and dorsal views. A, *T. simulans;* B, *T. grandiflora;* C, *T. ferreyrae;* D, *T. atacamensis;* E, *T. tacnensis;* F, *T. elongata;* G, *T. hunteri;* H, *T. litoralis;* I, *T. conspicua;* J, *T. paronychioides;* K, *T. galapagoa;* L, *T. nesiotica;* M, *T. darwinii.*

straight hairs appressed at various angles, these overlaid with antrorsely appressed or sharply inclined larger stiff bristles to 0.7 mm. long with thickened mineralized bases; lower surfaces somewhat more densely pubescent; petioles filiform, 0.5–1.5 mm. long with spreading hairs to 0.5 mm. long. Inflorescences terminal compact bracteate cymes, flowers appearing in conspicuous globose clusters 1.0–2.0 cm. across, the bracts linear to filiform, often resembling the calyx lobes. Calyces deciduous, enclosing the fruits, 5.0–7.5 mm. long, plumose with spreading thin stiff bristles to 1.3 mm. long on outer surfaces and upper half of inner surfaces; lobes unequal, free 4/5 the length, lanceolate, the apices filiform. Corollas opening in the morning and falling in the evening, pink to purple, 5.0–7.7 mm. long; villulose on outer surface near margin; the buds villulose. Stamens adnate to the corolla tube ca. 1/5 the length from base to limb, the veins below the points of attachment winged. Styles 2.1–3.3 mm. long, cleft 1/7–1/4 the length. Fruits (Figure 9B) single nutlets, ovoid-obpyriform, 1.8–2.5 mm. long, 0.9–1.2 mm. across, with tiny hairs spreading at the apex, retrorsely appressed and becoming more sparse below the apex to about the middle; exocarp thin, not indurated, dorsal surfaces purplish-black and shiny, ventral surfaces brown with a membranous tissue formed from 3 aborted mericarps. Chromosome number, $n = 9$.

DISTRIBUTION: *Tiquilia greggii* is found in xeric regions of southern New Mexico and trans-Pecos Texas, and in Mexico in eastern Chihuahua; Coahuila; northeastern Durango; eastern Nuevo Leon; northern San Luis Potosí; and northern Zacatecas (Figure 12). It grows on hilltops or slopes or desert flats in gypseous or limestone, often rocky soils with *Euphorbia antisyphilitica, Fouquieria splendens,* and species of *Agave, Larrea, Leucophyllum, Nerisyrenia, Prosopis,* and *Yucca,* and various cacti and grasses. It is often the dominant plant and usually does not grow in close proximity with other plants. It grows with four other species of *Tiquilia: T. canescens, T. gossypina, T. hispidissima,* and *T. mexicana,* and is geographically sympatric with *T. purpusii* and *T. turneri.*

Flowering season is April to November, whenever there is enough moisture.

In Mexico, it is called Yerba de la Cachucha and Regeneradora, and is used medicinally to treat gonorrhea (*Kelly 829,* UC).

Tiquilia greggii differs from all other *Tiquilia* species in (1) its

erect, shrubby habit. *Tiquilia turneri* and *T. tuberculata* are woody subshrubs, but not erect. The same is true of other taxa which are sometimes woody. (2) Reduction of nutlets to one by abortion of 3 ovules. (3) Adaptation for wind dispersal of the seed from a terminal inflorescence by retention of a single nutlet in a plumose calyx which falls when mature. The leaves resemble those of *T. canescens* and *T. mexicana,* while the inflorescence resembles that of the species of western North America and South America. *Tiquilia greggii* shows no close affinity to any other species of *Tiquilia* and can be easily identified at a glance.

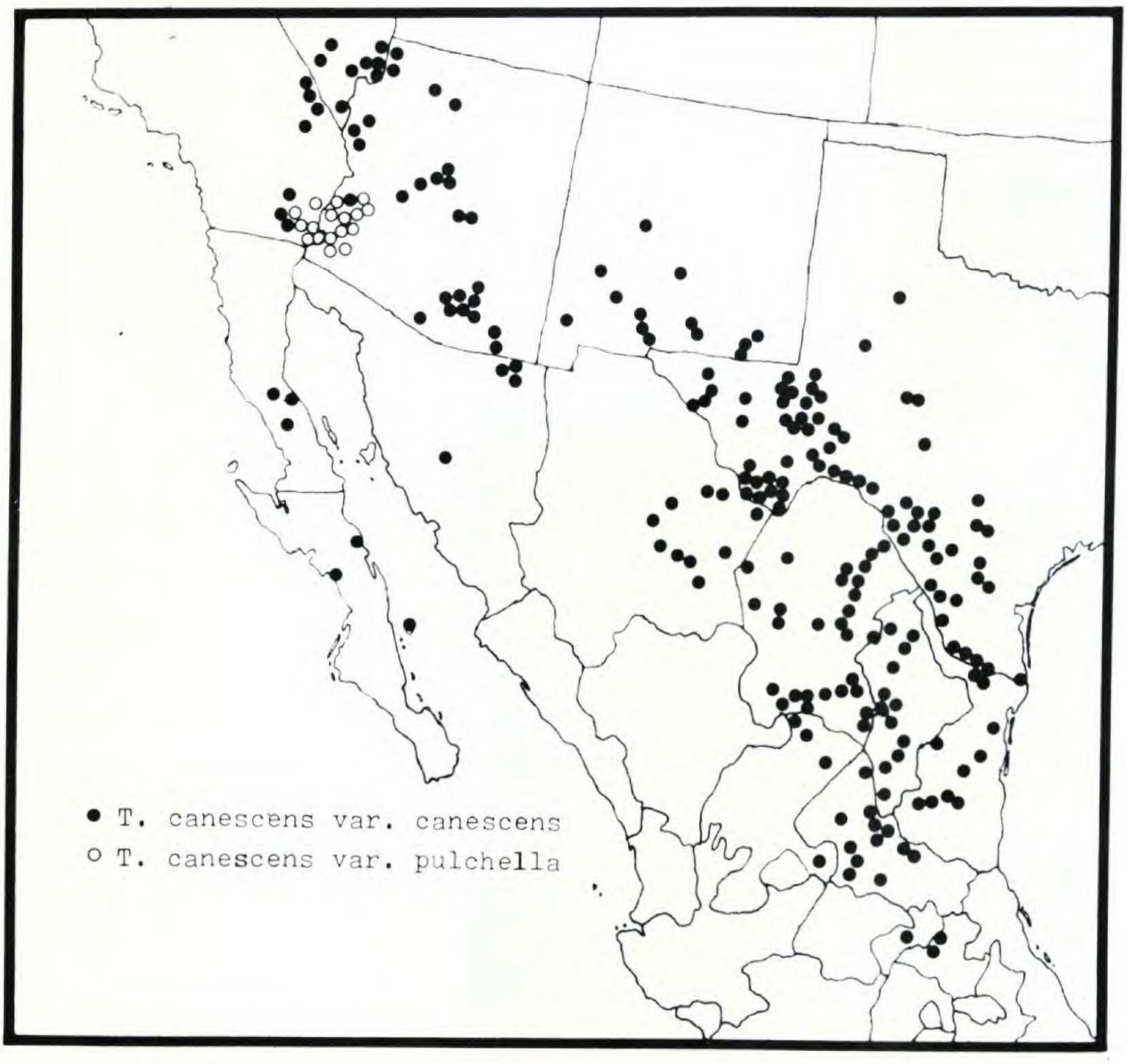

Figure 11. Distribution of *Tiquilia canescens* var. *canescens* and *T. canescens* var. *pulchella.*

Torrey and Gray (1857) chose the generic name *Ptilocalyx* from the Greek *Ptilo,* meaning down, feather, or wing, referring to the plumose calyx. This appropriately descriptive epithet is retained as the sectional name.

1c. **Tiquilia** sect. **Eddya** Gray, Proc. Am. Acad. **5:** 340. 1862.

TYPE SPECIES: *Tiquilia hispidissima* (Torrey & Gray) A. Richardson.

Procumbent or spreading, herbaceous, suffrutescent or fruticose. Leaves solitary at the nodes and in clusters on short branches or the stem apices; blades linear, oblong, narrowly ovate-obovate and needle-like, or ovate, bristly. Flowers solitary, axillary, or in small clusters with the leaves. Calyces persistent. Fruits lobed, of 1–4 nutlets; nutlets ovoid or obpyriform, somewhat indurated and colliculate or tuberculate, or smooth, not indurated. Chromosome number, $n = 9$ (*Tiquilia purpusii* with aneuploids, $n = 8$).

This is the most widespread section, including seven species of North America.

KEY TO THE SPECIES OF TIQUILIA SECT. EDDYA

a. Leaf blade length three times the width or more, petiole short, elliptic-rectangular. ..... b.
  b. Nutlet attachment scar narrow (0.2 mm. or less), open only above the middle or tapering to a point near the base; the bud glabrous or glandular. .... c.
    c. Nutlet white-colliculate, granular, or smooth; corolla winged below stamen attachments, the bud glandular or glabrous. ..... d.
      d. Nutlet black, smooth or granular, not indurated. ..... 6. *T. turneri.*
      d. Nutlet black, white-colliculate, indurated. ..... 8. *T. gossypina.*
    c. Nutlet white-tuberculate; corolla not winged below stamen attachments, the bud glandular. ..... 5. *T. tuberculata.*
  b. Nutlet attachment scar broad (0.3–0.5 mm.), open well below the middle; the bud villulose. ..... e.
    e. Leaf 5.0–17.0 mm. long, 1.1–4.2 mm. broad, blade obovate to narrowly obovate, petiole densely ciliate; nutlet obpyriform to ovoid, 1.5–2.0 mm. long, with white or brown collicula 0.04 mm. across or less. . 3. *T. latior.*
    e. Leaf 4.0–8.0 mm. long, 0.5–2.0 mm. broad, blade linear to narrowly obovate, petiole not noticeably ciliate; nutlet ovoid, 1.0–1.5 mm. long, with white collicula 0.05 mm. across or more. ..... 4. *T. hispidissima.*
a. Leaf blade length twice the width or less, petiole filiform at least in part. ..... f.
  f. Nutlet dark brown or black, the attachment scar and suture running straight from apex to base; leaf blade usually cinereous, upper surface with two kinds of hairs. ..... 7. *T. mexicana.*

f. Nutlet greenish or slate color, the attachment scar and suture running obliquely from apex to base; leaf blade usually green, upper surface with one kind of hair. ..... 9. *T. purpusii.*

3. **Tiquilia latior** (I. M. Johnston) A. Richardson, Sida **6:** 236. 1976.

Coldenia hispidissima (Torrey & Gray) Gray, var. *latior* I. M. Johnston, Contr. Gray Herb. **68:** 92. 1923. TYPE: **Nevada:** CLARK CO.[2] Muddy Valley, 1700 ft., 16 May 1906, *Kennedy & Goodding 79.* (Holotype, GH! Isotypes, ARIZ! F! UC! US!).

Herbaceous to suffrutescent, procumbent to decumbent, forming mats to 5.0 dm. broad from a woody taproot; caudices to 1.0 cm. thick; branches villous with large pungent spreading bristles to 1.9 mm. long with thickened mineralized bases. Leaves (Figure 6C) in clusters on short, brittle branches, 5.0–17.0 mm. long, 1.1–4.2 mm. broad; blades obovate, occasionally linear; upper surfaces bright green and prickly with large bristles 0.8–2.2 mm. long having thickened mineralized bases, or sometimes also minutely scabrous to villulose and cinereous; lower surfaces scabrous along the midrib; petioles very short, elliptic or somewhat rectangular, abaxial surfaces glabrous except for several large pungent bristles, rarely also villulose, the margins densely ciliate with long and short bristles, giving a white cottony appearance to the basal area of the leaf clusters on the lower surfaces. Flowers axillary, solitary or few. Calyces villous and ciliate, 3.0–4.0 mm. long; lobes lanceolate, free 2/3–3/4 the length, with large bristles 0.5–1.0 mm. long at the apices. Corollas pink, sometimes white, pale blue, or purple, 4.0–7.5 mm. long; the buds villulose. Stamens adnate to the corolla-tubes ca. 2/5 the length from base to limb. Styles 1.7–3.3 mm. long, cleft 1/13–1/3 the length. Nutlets (Figure 9C) 1–4, obpyriform, 1.5–2.0 (2.2) mm. long, (0.7) 0.8–1.1 mm. broad, indurated, dark brown to black with minute white and brown pustules, the attachment scars open, 0.3–0.5 mm. across at the apices, extending well below the middle. Chromosome number, $n = 9$.

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[2]Johnston (1923) designated Lincoln Co. as the type locality; however, McVaugh & Fosberg (1941) list Muddy Creek Valley in Clark Co., and no similar names in Lincoln Co. According to maps consulted by the present author Muddy River and Muddy Mountains are located in Clark Co.

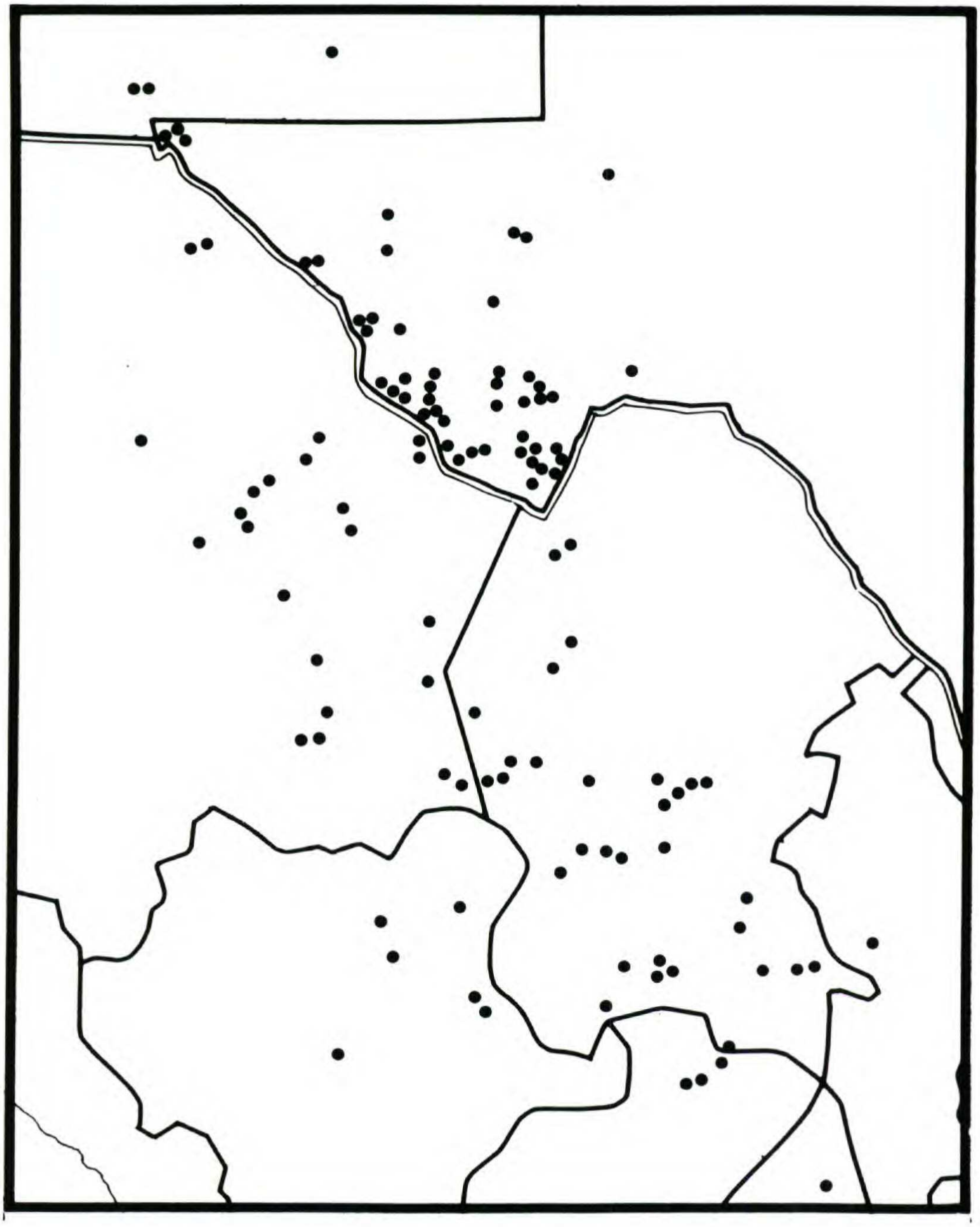

Figure 12. Distribution of *Tiquilia greggii*.

DISTRIBUTION: *Tiquilia latior* grows in red sandy soil, clay flats, and gypsum sand in the Colorado and Little Colorado River basins in Arizona, Nevada, and Utah (Figure 13) in association with *Astragalus, Atriplex, Ephedra, Juniperus, Larrea, Phacelia,* and *Stanleya.* It is geographically sympatric with *Tiquilia canescens, T. nuttallii,* and *T. plicata,* but it has not been reported growing with any of these species.

Flowering season is March through September.

The Supai Indians call this plant Ka-áw. They boil the roots to make a tea which they drink for stomach trouble (*Clover 5262,* GH).

Johnston (1923) treated *Tiquilia latior* as a foliar variation of *T. hispidissima* with a consistently wider leaf. The two taxa are treated here as separate species because they are disjunct and have diverged morphologically. The two taxa are, in most cases, more easily distinguished morphologically than are *T. hispidissima* and *T. gossypina,* which were recognized and contrasted by Johnston (1961). The morphological characetrs presented in the above key can be used to distinguish the two species.

For an objective evaluation, the mean, standard deviation, and standard error for nutlet length were calculated for each species, using measurements from 81 collections of *Tiquilia latior* and 80 collections of *T. hispidissima,* avoiding duplication of collections from the same locality. At a confidence level of 99%, the mean nutlet length for *T. hispidissima* will lie between 1.26 and 1.34 mm., and the mean nutlet length for *T. latior* will lie between 1.74 and 1.84 mm.

4. **Tiquilia hispidissima** (Torrey & Gray) A. Richardson, Sida **6:** 236. 1976.

Eddya hispidissima Torrey & Gray, Senate Executive Doc. No. 78, 33rd Congr., 2nd Sess. **2:** 170, 171. *Pl. 9.* 1857. TYPE: Common on the Rio Grande about El Paso, 1852, *Wright 1557.* (Lectotype fragment #2, GH! Duplicate of lectotype fragment #2, GH!).

Coldenia hispidissima (Torrey & Gray) Gray, Proc. Am. Acad. **5:** 340. 1862.

Herbaceous to suffrutescent, procumbent to decumbent, forming mats to 6.0 dm. broad from woody taproots (Figure 14); caudices to 1.5 cm. thick; young branches hispidulous-appressed with occasional spreading bristles. Leaves (Figure 6D) in clusters on short, brittle branches, 4.0–8.0 mm. long, 0.5–2.0 mm. broad; blades linear, occasionally narrowly lanceolate; upper surfaces usually green,

prickly with large bristles 0.5–2.4 mm. long having thickened mineralized bases, sometimes scabrous and lightly cinereous; lower surfaces scabrous along the midrib; petioles very short, elliptic or somewhat rectangular, glabrous, sometimes minutely scabrous, with pungent bristles along the margins. Flowers axillary, solitary. Calyces 2.5–4.0 mm. long, ciliate or villous with scattered sharp bristles 0.9–1.5 mm. long; lobes narrowly triangular or subulate, free 1/2–3/4 the length, inner surfaces lined with antrorsely appressed hairs. Corollas opening in the morning and falling in the evening; pink, rarely purple or white, with yellow throats; the tubes sometimes cylindrical, 2.5–6.5 mm. long; the buds villulose. Stamens adnate to the corolla tubes ca. 1/2 the length from base to limb. Styles 1.5–4.2 mm. long, cleft 1/10–1/4 the length. Nutlets (Figure 9D) 1–4, ovoid, 1.0–1.5 (1.7) mm. long, 0.7–1.1 (1.2) mm. broad, somewhat indurated, yellow to brown or sooty with white pustules ventrally, white-colliculate dorsally, the attachment scars open, 0.3–0.4 mm. across at the apices, extending well below the middle. Chromosome number, $n = 9$.

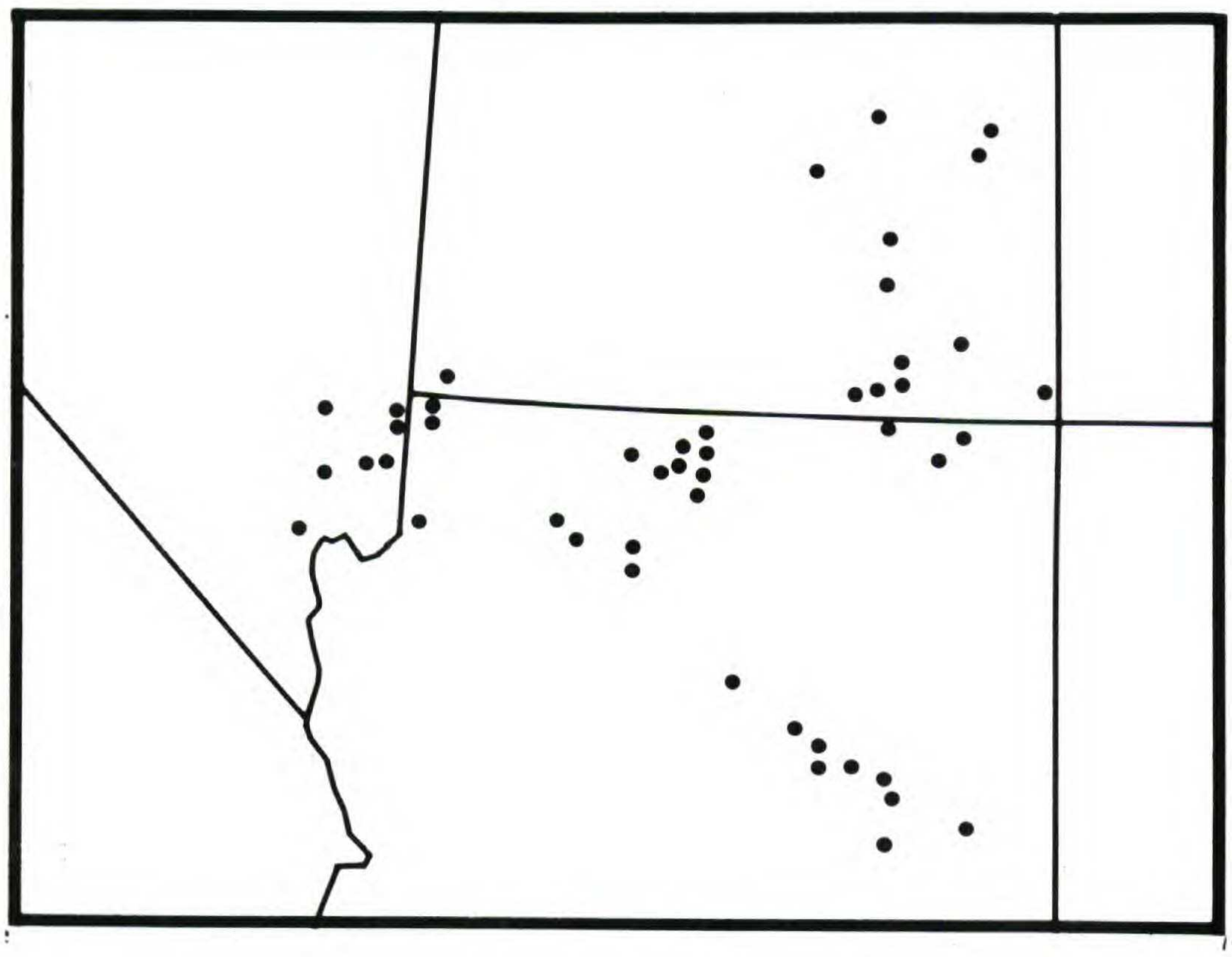

Figure 13. Distribution of *Tiquilia latior*.

Wright 1557 (GH) is a mixed collection of *Tiquilia hispidissima* and *T. gossypina.* The description and the accompanying illustrations contain elements of both species although both more closely correspond with *T. hispidissima.* On both herbarium specimens from the Gray Herbarium, fragment #1 is *T. gossypina* and fragment #2 is *T. hispidissima.* Consequently fragment #2 (GH) is designated the lectotype. A third herbarium specimen exists of *Wright 1557* (F!) but this has only *T. gossypina* and is eliminated as a type.

DISTRIBUTION: *Tiquilia hispidissima* occurs mainly in gypseous soils, occasionally calcareous soils in xeric regions of central New Mexico and trans-Pecos Texas, and in Mexico in eastern Chihuahua and western Coahuila (Figure 15). It grows in association with *Argemone turnerae, Bouteloua breviseta,* and species of *Atriplex, Chilopsis, Dasylirion, Fouquieria, Gutierrezia, Juniperus, Larrea, Nerisyrenia, Opuntia, Prosopis, Selinocarpus, Sporobolus, Suaeda,* and *Yucca.* It has been found *in situ* with 4 other species of *Tiquilia: T. canescens, T. gossypina, T. greggii,* and *T. mexicana;* and it is geographically sympatric with *T. tuberculata* and *T. turneri.*

This species flowers April through January.

Tiquilia hispidissima is distinguished from *T. gossypina* by the usually green, linear leaves with the petioles glabrous or scabrous but never villous; by the unappendaged corollas; and by the yellow to sooty nutlets with broad attachment scars. Comparisons with *T. latior* are made in the discussion of that species.

5. **Tiquilia tuberculata** A. Richardson, Sida **6:** 237. 1976. TYPE: **Mexico:** NUEVO LEON. Km. 100 on hwy. from Monterrey to Monclova, 28 Aug. 1973, *Richardson 2181.* (Holotype, TEX! Isotypes, ARIZ! CAS! F! GH! MEXU! MICH! NY! RM! UC! US!).

Small, gnarled and twisted subshrubs to 2.0 dm. tall and 3.0 dm. across, the caudices to 0.8 cm. thick; young stems densely villous and woolly to moderately villous. Leaves (Figure 6E) on short, brittle branches, 2.8–4.5 mm. long, 0.6–1.2 mm. broad; blades linear to oblong, upper and lower surfaces green, with large bristles 0.8–2.2 mm. long, rarely lightly cinereous and minutely hispid with hairs ca. 0.2 mm. long; petioles very short, elliptic or somewhat rectangular, minutely ciliate, abaxial surfaces glabrous or rarely lightly villous. Flowers axillary, solitary. Calyces 2.0–2.5 mm. long, ciliate, with occasional stiff bristles to 0.5 mm. long; lobes narrowly tri-

angular to subulate, free ca. 2/3 the length, inner surfaces with antrorsely appressed hairs. Corollas opening in the morning and falling in the evening; lilac to milk-white, 4.5–6.0 mm. long; the buds glandular. Stamens adnate to the corolla tube ca. 1/3 the length from base to limb, veins below the point of attachment not winged. Styles 2.5–3.2 mm. long, cleft 1/5–1/2 the length. Nutlets (Figure 9E) 1–4, ovoid, 1.0–1.1 mm. long, 0.5–0.6 mm. broad, black with white tubercles, the attachment scar slightly open, 0.1–0.15 mm. across at the apex, tapering to a point along a ridge ca. half way to the base, the ridge continuing to the base.

DISTRIBUTION: Two populations ca. 20 km. apart are known, both from northwestern Nuevo Leon, Mexico (Figure 16). *Tiquilia tuberculata* grows in gypseous soils in association with *Fouquieria, Frankenia, Larrea, Lycium, Nerisyrenia, Opuntia, Selinocarpus, Sporobolus,* and *Suaeda.* It is geographically sympatric with *Tiquilia canescens, T. mexicana,* and *T. turneri,* but it has not been reported to be growing in mixed populations with any of these species.

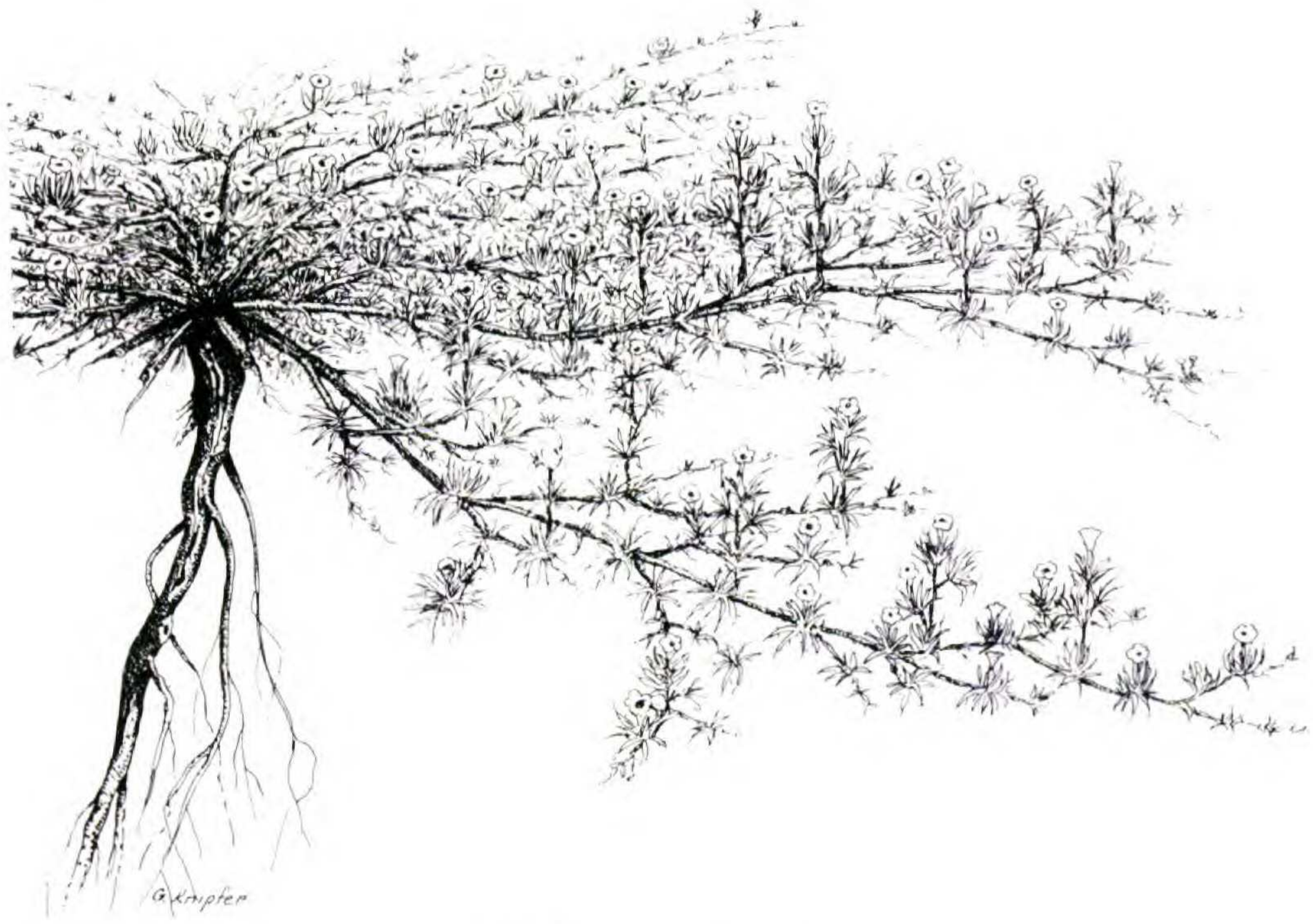

Figure 14. Drawing of habit of *Tiquilia hispidissima.*

Flowering times, known from limited collecting data, are March, July, and August.

The most outstanding characteristic of this species is the white-tuberculate ornamentation on the nutlets. In all other species of *Tiquilia* the nutlets are aculeate, colliculate or pusticulate, granulate, or lacking in ornamentation. Nutlet and floral characters are the most convenient in distinguishing *T. tuberculata* from *T. gossypina* and *T. turneri.*

6. **Tiquilia turneri** A. Richardson, Sida **6:** 237, 238. 1976. TYPE: **Mexico:** COAHUILA. 12.4 mi. S and 2 mi. W of Cuatro Ciénegas, in gypsum dunes, 29 Jun. 1971, *Richardson 1595.* (Holotype, TEX! Isotypes, ARIZ! CAS! F! GH! MEXU! MICH! NY! RM! UC! US!).

Gnarled and twisted subshrubs (Figure 17) forming mounds to 9.0 dm. across, the caudices to 10.0 cm. thick; juvenile forms procumbent; young stems densely villous and woolly to moderately villous; leaf clusters on short brittle branches, the internodes between the branches on old plants sharply reduced in length and hidden by the leaf clusters. Leaves (Figure 6F) 2.5–5.5 mm. long, 0.6–1.5 mm. broad; blades linear to oblong; upper and lower surfaces densely villous and cinereous to lightly villous and green, with large bristles 0.7–1.7 mm. long; petioles very short, elliptic or somewhat rectangular, heavily villous over all or ciliate. Flowers axillary, solitary. Calyces 2.0–3.0 mm. long, densely villous or ciliate; lobes narrowly triangular to subulate, free ca. 1/2 the length, each with soft antrorsely appressed hairs on the inner surface and with 1 or 2 stiff apical bristles 0.7–1.7 mm. long. Corollas opening in the morning and falling in the evening; violet with yellow throats, 3.4–6.5 mm. long; the buds glandular. Stamens adnate to the corolla tube ca. 1/3 the length from base to limb, the veins winged below the point of attachment. Styles 1.5–3.3 mm. long, cleft 1/6–1/2 the length. Nutlets (Figure 9F) 1 or 2, ovoid, 0.8–1.5 mm. long, 0.6–0.8 mm. broad, shiny black, smooth or granular, not indurated, the attachment scars slightly open, 0.1–0.15 across at the apex, tapering to a point at the base. Chromosome number, $n = 9$.

The specific epithet is given in recognition of B. L. Turner who first collected this taxon and called it to my attention.

DISTRIBUTION: Two populations, separated by about 160 kilometers, are known (Figure 16). The first to be known grows in and around shifting gypsum dunes about 25 km. southwest of Cuatro Ciénegas, Coahuila, Mexico, where it is the dominant plant growing with *Dasylirion, Nerisyrenia, Selinocarpus,* and *Yucca.* The second population grows in a gypseous area about 100 km. northwest of Monterrey, Nuevo Leon, Mexico, the dominant plant growing with *Dyssodia acerosa, Tiquilia mexicana,* and species of *Larrea, Opuntia,* and *Yucca.* Although *Tiquilia turneri* has been observed growing with only one other species of *Tiquilia* (*T. mexicana*), it is geographically sympatric with *T. canescens, T. gossypina,* and *T. greggii.*

This species flowers May through October.

There are two distinct growth forms, depending on the age of the plants and possibly the substrate. Old shrubby plants, which grow to 9.0 dm. across and 4.0 dm. high with caudices to 10.0 cm. diameter, are found in the gypsum dunes near Cuatro Ciénegas. They show marked reduction in internode length, bringing the leaf clusters close together and hiding the stem. There is a reduction in leaf size (2.5–4.5 mm. long) and length of bristles on the leaves and calyces (0.7–1.0 mm. long), and there is an abundance of fine appressed hairs giving the leaves a cinereous appearance and completely covering the young stems giving a white woolly appearance.

Younger plants growing near the base of the same gypsum dunes are herbaceous and prostrate, growing to 4.0 dm. across, with slightly larger leaves (to 5.5 mm. long), longer internodes (0.5–1.0 cm. long), and longer bristles (1.0–1.7 mm. long) on the leaves and calyces. The leaves are usually green because of reduced pubescence; the petioles are villous to glabrous; and the fine hairs only partially cover the young stems.

The Nuevo Leon population is much like that of the gypsum dunes in Coahuila. The plants are small subshrubs with larger leaves, less pubescence, and slightly smaller nutlets.

Tiquilia turneri is closely related to *T. gossypina,* the two species having several floral and vegetative characters in common. *Tiquilia turneri* is distinguished from *T. gossypina* by its smaller leaves and flowers, the shrubby habit and often reduced stem internodes, and the smaller and somewhat narrower nutlets which have a thin and relatively soft and smooth pericarp.

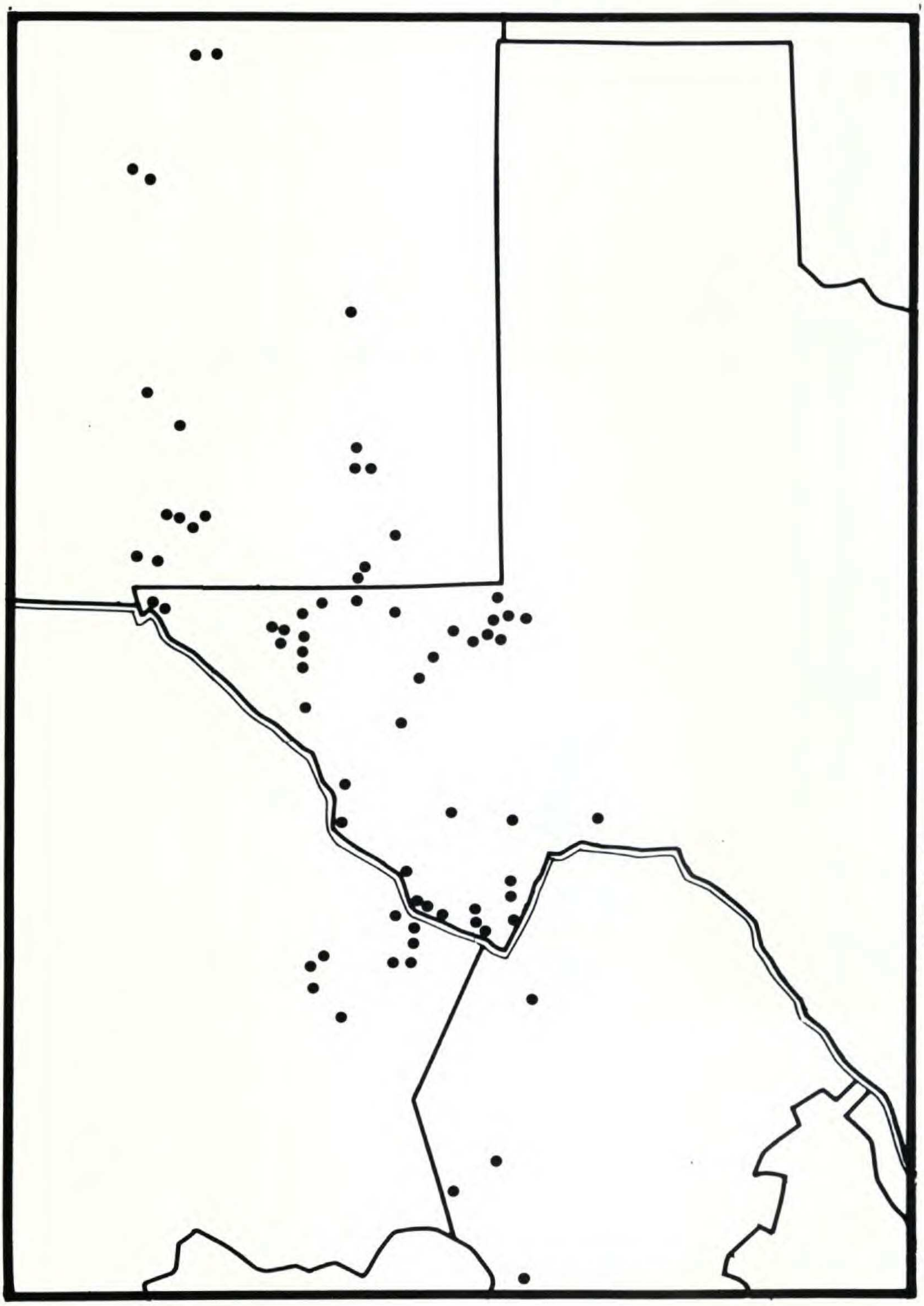

Figure 15. Distribution of *Tiquilia hispidissima.*

7. **Tiquilia mexicana** (Watson) A. Richardson, Sida **6:** 236. 1976.

Coldenia mexicana Watson, Proc. Am. Acad. **18:** 120. 1883. TYPE: **Mexico:** COAHUILA. In the mountains east of Saltillo, Aug. 1880, *Palmer 872.* (Holotype, GH! Isotypes, F! NY! US!).

Coldenia tomentosa Watson, Proc. Am. Acad. **18:** 120. 1883. TYPE: **Mexico:** COAHUILA. In the Sierra Madre 40 mi. south of Saltillo, Mar. 1880, *Palmer 864.* (Holotype, GH! Isotype, US!).

Coldenia mexicana var. *tomentosa* (Watson) I. M. Johnston, Wrightia **2:** 159. 1961.

Herbaceous, procumbent, forming mats to 1 meter across from woody caudices; caudices to 1.0 cm. thick; branches cinereous, densely villous, with occasional stiff bristles to 1.0 mm. long. Leaf blades (Figure 6G) ovate to elliptic, 6.0–10.5 mm. long, 2.5–5.3 mm. broad, upper and lower surfaces cinereous and densely villous (rarely lightly villous and green), with stiff bristles 1.0–2.0 mm. long with thickened mineralized bases; petioles filiform distally, broader near the base, 1.6–6.0 mm. long, villous, with spreading bristles to 1.2 mm. long. Flowers axillary, solitary, or in small bracteate clusters. Calyces 3.0–4.0 mm. long, densely villous or ciliate, with scattered sharp bristles to 1.0 mm. long; lobes lanceolate to subulate, free 2/3 the length, inner surfaces with antrorsely appressed hairs. Corollas opening in the morning, falling in the evening; purple, violet or pink, often with a yellow throat, 5.0–9.0 mm. long; the buds glabrous, glandular, or villulose. Stamens adnate to the corolla tubes ca. 1/3 the length from base to limb, the veins below the points of attachment swollen or rarely winged. Styles 2.4–4.7 mm. long, cleft 1/4–1/2 the length. Nutlets (Figure 9G) 1 or 2, rarely 3, ovoid, 1.0–1.5 mm. long, 0.7–1.1 mm. broad, black with white collicula, the attachment scars slightly open to 0.2 mm., only above the middle. Chromosome number, $n = 9$.

DISTRIBUTION: *Tiquilia mexicana* occurs in southern trans-Pecos Texas, eastern Chihuahua, Coahuila, western Nuevo Leon, and northern Zacatecas (Figure 18), where it grows in both limestone and gypseous soils, always in xeric conditions and without evident competition, with the exception of other species of *Tiquilia.* It is often found growing with *T. canescens, T. gossypina, T. greggii, T. hispidissima,* and *T. turneri,* and is geographically sympatric with *T. purpusii* and *T. tuberculata.* It grows in association with *Agave, Flourensia, Fouquieria, Larrea, Opuntia,* and *Prosopis.*

Flowering season is February to November.

In Mexico, it is known as Oreja de Ratón.

Watson (1883) described *Coldenia tomentosa* as resembling *C. mexicana* but with thicker, more strongly revolute leaves, shorter petioles, and larger flowers and nutlets. These characters vary, and intermediate conditions are commonly found. Johnston (1961) recognized *C. mexicana* var. *tomentosa,* acknowledging only one sharp, decisive character, the villulose condition of the bud in the var. *tomentosa.* This character is variable, even within populations. Therefore *Tiquilia mexicana* is treated here as a variable species with no subdivisions.

Tiquilia mexicana has some characters in common with *T. gossypina,* in particular the nutlet characters, but it is distinguished from that species by its wider leaves, longer and slender petioles, and its herbaceous habit. The two species grow together and no hybrids have been detected.

8. **Tiquilia gossypina** (Wooton & Standley) A. Richardson, Sida **6:** 236. 1976.

Eddya gossypina Wooton & Standley, Contr. U. S. Nat. Herb. **16:** 164. 1913. TYPE: **New Mexico:** DONA ANA CO. Tortugas Mountain, Las Cruces, 2 Sep. 1894, *Wooton s.n.* (Holotype, US No. 690234. Fragment of holotype with photograph of holotype, GH!).

Coldenia gossypina (Wooton & Standley) I. M. Johnston, Wrightia **2:** 158. 1961.

Herbaceous to suffrutescent, procumbent to decumbent, forming mats to 6.0 dm. across from woody taproots; caudices to 1.5 cm. thick; young branches scabrous, strigose, or hispid. Leaves (Figure 6H) 3.3–11.7 mm. long, 0.6–2.3 mm. broad; blades narrowly obovate, sometimes linear; upper surfaces cinereous, occasionally light green, villous or scabrous, prickly with large bristles 0.8–2.0 mm. long having thickened mineralized bases; lower surfaces scabrous, especially along the prominent midribs, usually also villous, rarely glabrous; petioles very short, elliptic or somewhat rectangular, usually villous, sometimes glabrous and shiny brown on abaxial surfaces, with large pungent bristles at the margins. Flowers axillary, solitary. Calyces 2.0–3.7 mm. long, villous or ciliate, with scattered sharp bristles to 1.7 mm. long; lobes narrowly triangular to subulate, free 1/2–2/3 the length, inner surfaces with antrorsely appressed hairs. Corollas opening in the morning and falling in the evening; purple to pink or rarely white, with yellow throats, 4.3–11.5 mm. long; the buds glabrous or glandular.

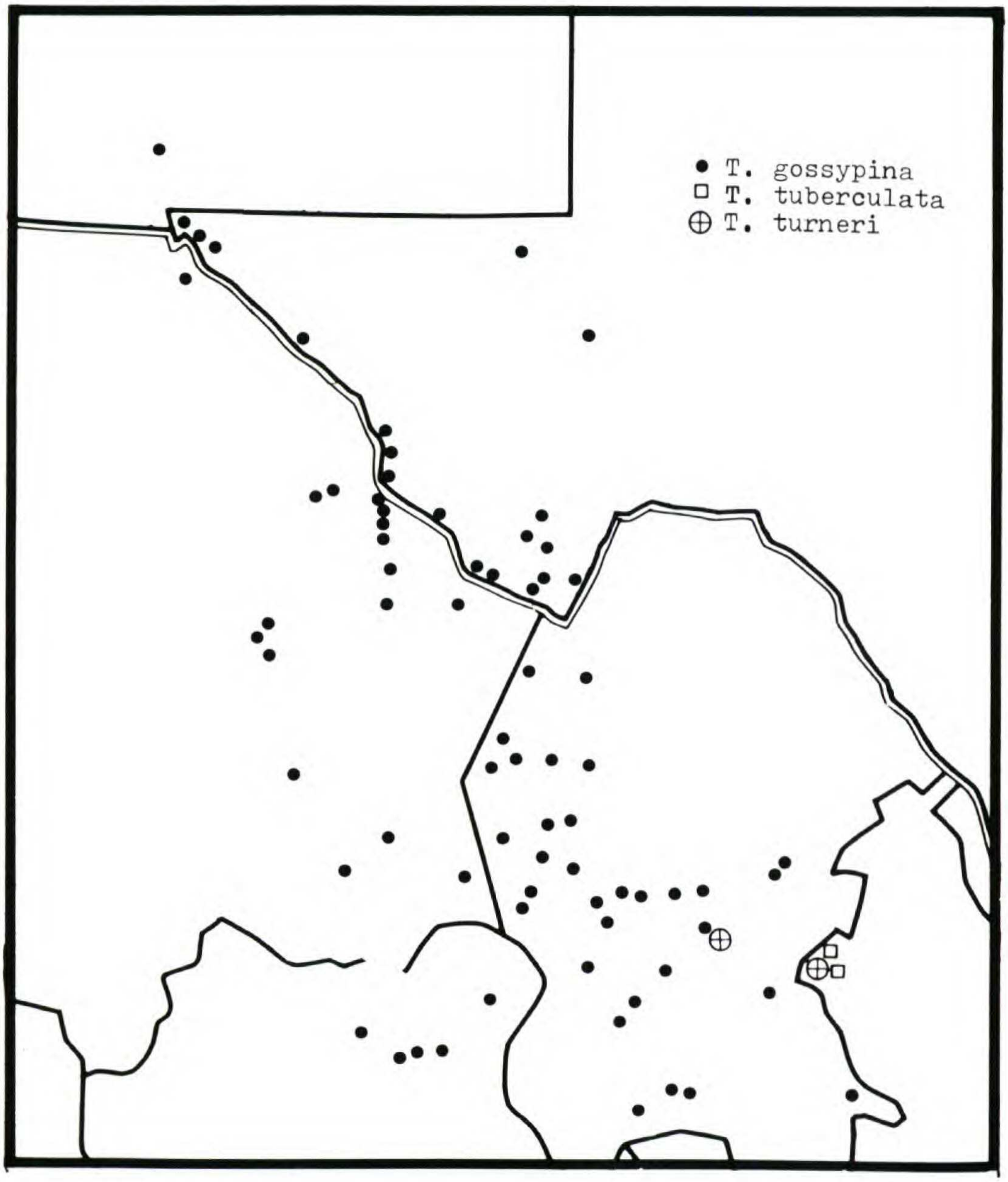

Figure 16. Distribution of *Tiquilia gossypina*, *T. tuberculata*, and *T. turneri*.

Stamens adnate to the corolla tubes ca. 1/3 the length from base to limb, the veins below the points of attachment winged. Styles 2.1–6.5 mm. long, cleft 1/4–1/3 the length. Nutlets (Figure 9H) 1–4, ovoid, (0.9) 1.1–1.3 (1.5) mm. long, (0.7) 0.8–1.0 (1.3) mm. broad, somewhat indurated, black with white pustules ventrally, white-colliculate dorsally, the attachment scars slightly open, to 0.2 mm., only above the middle. Chromosome number, $n = 9$.

DISTRIBUTION: *Tiquilia gossypina* occurs in southern New Mexico, and adjacent trans-Pecos Texas, especially near the Mexican border; in Mexico it occurs in eastern Chihuahua, Coahuila, and northern Durango (Figure 16), in association with *Fouquieria, Larrea, Nama, Nerisyrenia, Selinocarpus,* and *Yucca.* It usually grows in gypseous soils and competes only with other species of *Tiquilia.* It is often found growing with *T. canescens, T. greggii, T. hispidissima,* and *T. mexicana.* This investigator has seen it growing in the same clump with *T. canescens* and *T. hispidissima,* all flowering, and it is geographically sympatric with *T. purpusii* and *T. turneri.*

Tiquilia gossypina flowers March through November. It appears to be less gypsum-tolerant than *T. hispidissima, T. tuberculata,* and *T. turneri.* Suffrutescent forms are often found in areas of high gypsum concentration, although growing alongside herbaceous forms. The suffrutescence is usually correlated with a marked reduction in leaf size.

A dimorphic population of *Tiquilia gossypina* was found growing along the roadside in Coahuila, Mexico, 40 kilometers north of Monclova. One hundred samples were taken for populational studies, 50 from each side of the highway (*Richardson 1643A & 1643B*). Two distinct forms were growing intermingled, with no intergradation observable in the field. One form was typical *T. gossypina;* the other showed a marked vegetative similarity to *T. hispidissima.*

Morphological studies in the laboratory showed a uniformity of size, shape, color, and ornamentation of the nutlets among all samples, corresponding with *Tiquilia gossypina.* Essential floral characters were also those of *T. gossypina.* The nutlet and floral characters have proved to be reliable within the genus, whereas the vegetative characters are often variable. Therefore, in the absence of experimental data, both forms must be referred to *T. gossypina,* although the possibility that the plants represent F_1 hybrids cannot be ruled out.

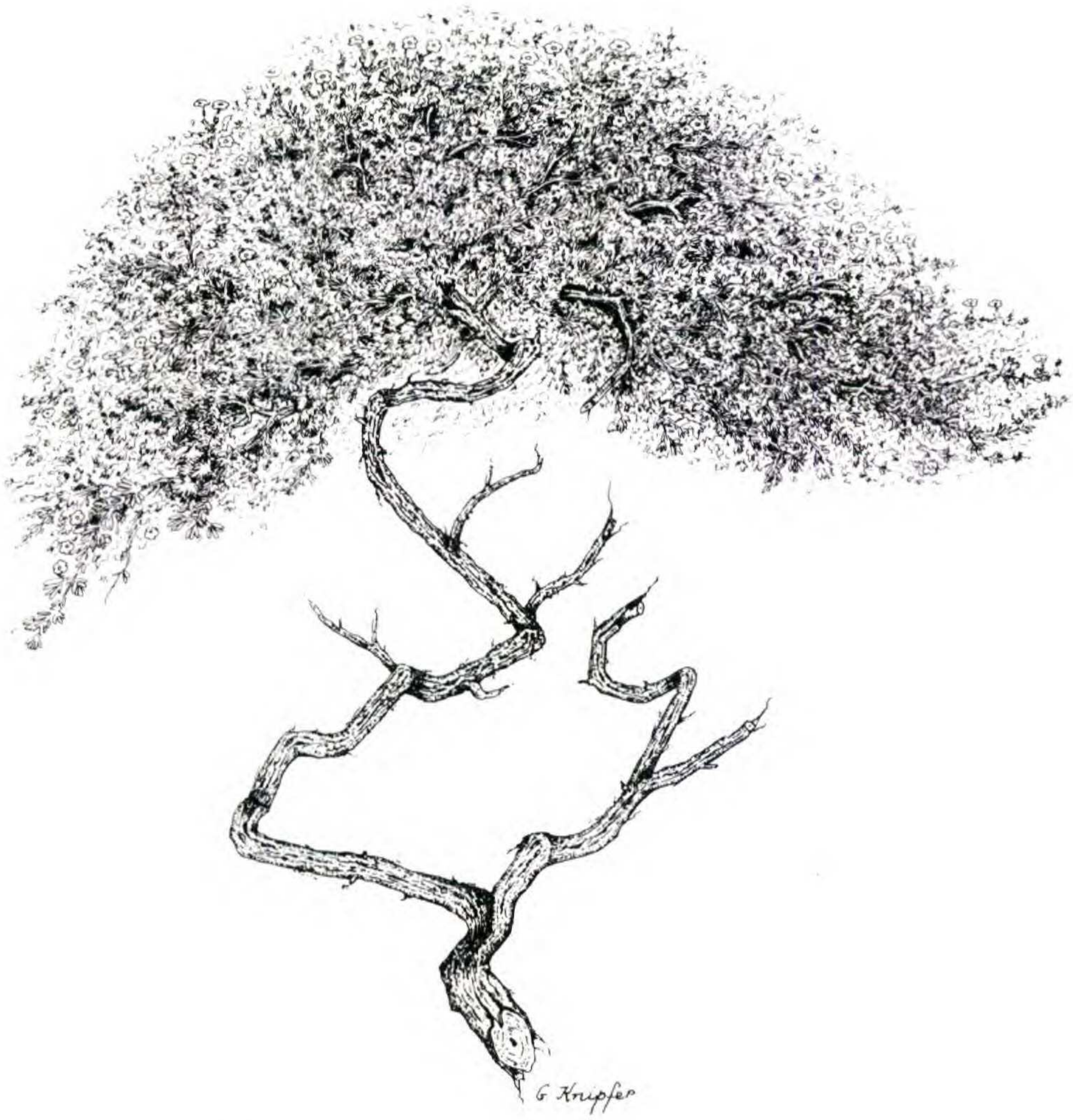

Figure 17. Drawing of habit of *Tiquilia turneri*.

Several populations in southern Chihuahua and northern Durango are in question (*Correll & Johnston 20228, Gentry 8628, Johnston 7762, Juzepczuk 637, Ripley & Barneby 13953, Shreve 8790*). Field studies of these populational sites were not made; therefore, all observations were necessarily made from preserved herbarium material. Typical *Tiquilia gossypina* has not been collected with these populations, although it has been collected in nearby parts of Chihuahua and Durango.

These populations are uniform, vegetatively like *Tiquilia hispidissima* in the extreme. This evidently influenced Johnston to identify his collections as forms related to *T. hispidissima*. The

floral parts, however, are those of *T. gossypina* and the nutlets, although not identical with *T. gossypina,* are quite like this species. Neither the floral nor the nutlet characters resemble *T. hispidissima.* Field studies and experimental work are needed to clarify the relationships of these populations. For the present they are included with *T. gossypina.*

Tiquilia gossypina is best distinguished from *T. hispidissima,* with which it has often been confused, by (1) its black nutlets with narrow attachment scar; (2) the glabrous or glandular condition of the bud; (3) the winged condition of the veins below the stamen attachment to the corolla; and (4) the usually villous condition of the petiole.

9. **Tiquilia purpusii** (Brandeg.) A. Richardson, Sida **6:** 237. 1976.

Coldenia purpusii Brandeg., Univ. Calif. Publ. Bot. **4:** 186. 1911. TYPE: **Mexico:** SAN LUIS POTOSÍ. Minas de San Rafael, Nov. 1910, *Purpus 4857* (Holotype, UC! Isotypes, F! GH! US!).

Herbaceous and procumbent, forming mats to 6.0 dm. across from woody caudices; caudices to 1.2 cm. thick; branches with abundance of fine spreading hairs to 1.2 mm. long, often also villulose. Leaf blades (Figure 6I) green, narrowly ovate to ovate, 5.0–10.0 mm. long, 1.5–5.5 mm. broad; upper surfaces with fine, antrorsely inclined bristles to 1.2 mm. long with thickened, mineralized bases, midveins somewhat sunken, lateral veins not conspicuous; lower surfaces with higher concentration of bristles and with midveins and lateral veins prominent; petioles filiform, 1.5–6.5 mm. long, densely covered with stiff, spreading hairs to 1.2 mm. long, giving a white cottony appearance to the petiole area of the leaf clusters on the lower surfaces. Flowers axillary and solitary or several, or in small clusters subtended by bracts. Calyces persistent, 3.0–5.5 mm. long with an abundance of slightly antrorsely inclined stiff bristles to 1.0 mm. long, especially toward the base; lobes narrowly triangular, free ca. 3/4 the length, with short antrorsely appressed hairs on the inner surfaces. Corollas opening in the morning and falling in the evening; light blue to amethyst with darker throats, rarely ivory-white, 5.0–7.2 mm. long; the buds glabrous, minutely glandular and villous, or with spreading bristles to 0.2 mm. long. Stamens adnate to the corolla tubes ca. 1/4 the length from base to limb, the veins below the points of attachment usually swollen, sometimes faintly winged. Styles 2.2–4.9 mm.

long, cleft 1/8–1/4 the length. Nutlets (Figure 9I) 1–4, usually 1 or 2, often arranged spirally in the fruit, ovoid, 0.9–1.4 mm. long, 0.6–0.9 mm. broad, dark brown to slate-gray with white collicula, the attachment scars slightly open above the middle, to 0.1 mm. wide and 0.3 mm. long, the suture running obliquely to the base. Chromosome numbers, $n = 9$; $n = 8$.

DISTRIBUTION: *Tiquilia purpusii* has the southernmost distribution of the North American species of *Tiquilia*, excepting for the widespread *T. canescens* (Figure 19). It grows in xeric sites in Mexico, occurring in southeastern Coahuila, southern Nuevo Leon, Querétaro, San Luis Potosí, southwestern Tamaulipas, and northeastern Zacatecas, in association with *Cordia, Jatropha, Larrea, Nama, Prosopis, Yucca,* and various grasses on gypseous or limestone soils. It is occasionally found competing successfully with grasses but usually does not grow in close proximity with other plants. *Tiquilia purpusii* grows with one other species of *Tiquilia, T. canescens,* and is geographically sympatric with *T. gossypina, T. greggii,* and *T. mexicana* at its northern limits of distribution.

Flowering seasons are January through March and June through December.

Among the species of southwestern United States and central Mexico, *Tiquilia purpusii* is notable for its bright green leaves and its nutlets with oblique sutures. The collicula are relatively larger on the nutlets of this species, and the exocarp is often a slate-gray color. Vegetatively, it resembles *T. cuspidata* of Sonora and Baja California, but the fruit characters are quite different. (*Tiquilia cuspidata* has black, granular nutlets with long, straight, wide attachment scars and with basally attached styles.) The species is quite distinct and is not likely to be confused with another.

Tiquilia subgen. **Tiquilia.** TYPE SPECIES: *Tiquilia dichotoma* (Ruiz & Pavon) Persoon.

Leaf margins entire or crenate. Nutlets ovoid, hemiovoid, or spheroid, smooth, minutely colliculate, minutely aculeate, or granular, the ornaments always smaller than 0.04 mm. across. Style attachments apical, sub-apical, sub-basal, or basal. Chromosome number, $n = 8$ (rarely aneuploid with $n = 9$), 16, 15, & 14.

Tiquilia sect. **Tiquiliopsis** Gray, Proc. Am. Acad. **5:** 340. 1862. TYPE SPECIES: *Tiquilia nuttallii* (Bentham ex Hooker) A. Richardson.

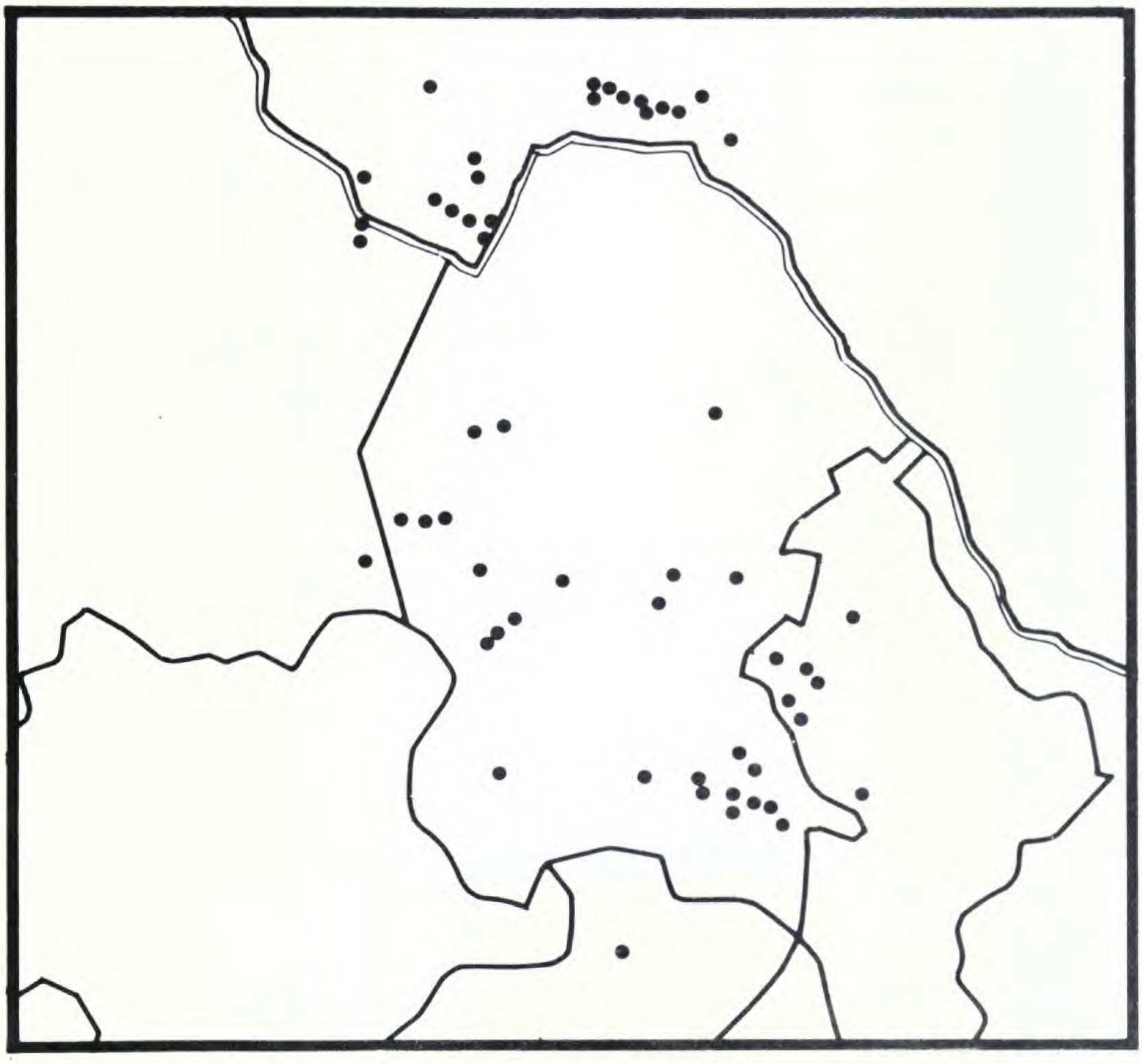

Figure 18. Distribution of *Tiquilia mexicana*.

Plants procumbent or spreading, herbaceous from woody caudices. Leaves in axillary or terminal clusters; blades elliptic, lanceolate, ovate-obovate or sub-orbicular, marginally entire. Flowers in clusters with the leaves. Calyces persistent. Corollas deciduous. Stamens unequal, included, adnate to the corolla tubes at 3 levels. Style attachments sub-apical, sub-basal, or basal. Fruits lobed, of 1–4 nutlets; nutlets ovoid or spheroid, indurated, smooth, granular, or minutely aculeate. Chromosome number, $n = 8$ (*Tiquilia palmeri* with aneuploids $n = 9$).

This section includes four species; three of them North American, in western United States and western Mexico; and one amphitropical disjunct species which occurs in western North America and again in South America, western Argentina.

KEY TO THE SPECIES OF TIQUILIA SECT. TIQUILIOPSIS

a. Leaf blade without crowded, deeply plicate lateral veins; nutlet smooth, granular, or minutely aculeate, brown or black, dull or shiny; style attachment sub-apical or basal. ..... b.
  b. Petiole filiform; nutlet brown or mottled grey, brown, and black, smooth or minutely aculeate. ..... c.
    c. Lateral veins of leaves at ca. 30° angle to the midrib; corolla 3.0–4.0 mm. long; style not exserted beyond calyx lobes, attachment sub-apical; nutlet ovoid. ..... 10. *T. nutallii.*
    c. Lateral veins of leaves at ca. 45° angle to the midrib; corolla 3.5–9.5 mm. long; style exserted beyond calyx lobes, attachment basal; nutlet spheroid. ..... 13. *T. palmeri.*
  b. Petiole ovate-trullate, sometimes filiform distally; nutlet black, granular. .. .. 12. *T. cuspidata.*
a. Leaf blade with 4–7 pairs of crowded, deeply plicate lateral veins; nutlet smooth, black, shiny; style attachment sub-basal. ..... 11. *T. plicata.*

10. **Tiquilia nuttallii** (Bentham ex Hooker) A. Richardson, Sida **6:** 236. 1976.

Coldenia nuttallii Bentham ex Hooker, Hooker's Jour. Bot. Kew Gard. Misc. **3:** 296. 1851. TYPE: **Utah:** UTAH CO. Sandy desert of muddy rivers near the great salt-lake Timpanagos (sic.), Aug. 1845, *Geyer 80.* (Holotype, K! Isotypes, K! TEX!).

Tiquilia parvifolia Nuttall ex Hooker, Hooker's Jour. Bot. Kew Gard. Misc. **3:** 296. 1851, *nomen. nud.* (A reference to a Nuttall manuscript.)

Tiquilia brevifolia Nuttall ex Torrey, Bot. Wilkes Exped. **2:** 410. 1874. TYPE: On the Walla-Walla River, Washington Territory (Holotype, GH!).

Tiquilia oregana Torrey, Bot. Wilkes Exped. **2:** 410. 1874, *nomen. nud., lapsus calami.*

Tiquiliopsis nuttallii (Bentham) Heller, Muhlenbergia **2:** 239. 1906.

Coldenia decumbens Hauman, Apuntes Hist. Nat. **1:** 55. 1909. TYPE: **Argentina:** MENDOZA. Terrenos arenosos del valle del Rio Tupungato, a 2500 metros de altitud, no lejos de Punta de Vacas, a principios de febrero de 1908, *L Hauman 268.* (Holotype, BA! Possible isotype, GH!.) (Herbarium label on holotype indicates 2350 meters altitude.)

Coldenia nevadensis Gand., Bull. Soc. Bot. France **65:** 61. 1918. TYPE: **California:** Ad Reno, 5 June 1894, *Hillman s.n.* (Holotype, LY! Isotypes, POM! RM!).

Procumbent or spreading, forming mounds to 3.0 dm. across; caudices to 0.5 cm. thick; older stems woody, the bark pale brown; young branches villous or pubescent with stiff appressed hairs to 0.2 mm. long, with scattered spreading or inclined bristles to 1.2 mm. long. Leaves (Figure 6J) in clusters at the nodes or stem apices; blades green or gray-green, ovate to elliptic, 3.8–9.5 mm. long, 2.2–7.8 mm. broad, with 2–3 pairs of lateral veins ascending

ca. 30° from the midrib; upper surfaces strigose and with scattered or abundant large antrorsely inclined bristles to 1.0 mm. long, especially along veins and margins; lower surfaces more densely pubescent with finer spreading or appressed hairs to 0.5 mm. long; petioles filiform, 2.5–8.5 mm. long, with abundant spreading hairs to 1.7 mm. long. Flowers in bracteate clusters, Calyces 2.5–4.0 mm. long, outer surfaces glistening, with short inclined or appressed hairs 0.1–0.3 mm. long, and larger spreading or antrorsely inclined bristles 0.5–1.5 mm. long; lobes narrowly triangular, free 2/3–3/4 the length, often ciliate, inner surfaces with antrorsely appressed hairs. Corollas white to violet with yellow throats, 3.0–4.0 mm. long, the tubes often constricted near the apices or rarely cylindrical; the buds glabrous or glandular. Stamens adnate to the corolla tubes ca. 1/3 the length from base to limb, veins below stamen attachments winged near bases of tubes, wings ca. 0.5 mm. long. Styles 1.0–2.3 mm. long, not exserted beyond the calyx, cleft 1/2–3/4 the length, attached to the nutlets sub-apically, 0.3–0.4 mm. below the nutlet apices. Nutlets (Figure 9J) 4, oblong-ovoid, 1.1–1.5 mm. long, 0.6–0.8 mm. broad, shiny and smooth (minutely colliculate under high magnification), gray, mottled brown or black. Cotyledons hippocrepiform (Gray, 1888). Chromosome number $n = 8$.

DISTRIBUTION: *Tiquilia nuttallii* occurs in northern Arizona, eastern and southern California, northwestern Colorado, southern Idaho, Nevada, eastern Oregon, Utah, eastern Washington, and southwestern Wyoming (Figure 20). It is usually found growing in desert sands or sandy loam, from below sea level to 2400 meters altitude, with associations of *Artemisia, Atriplex, Chrysothamnus, Juniperus, Larrea,* and *Pinus.* It grows with *T. palmeri* and *T. plicata* and is geographically sympatric with *T. canescens* and *T. latior.* Two collections, from north central New Mexico and Missouri, are no doubt recent introductions.

Tiquilia nuttallii is also found in South America (Figure 21) in northwestern Argentina in the provinces of Mendoza and San Juan. It occurs at altitudes of 1500–3050 meters, in sand and sandy clay in association with *Adesmia, Ephedra, Gilia, Glandularia, Hoffmanseggia, Larrea, Lycium, Nama, Senecio, Stevia, Stipa, Verbena,* and various cacti.

Tiquilia nuttallii has the southernmost distribution of the South American species and is the only species of *Tiquilia* known east of

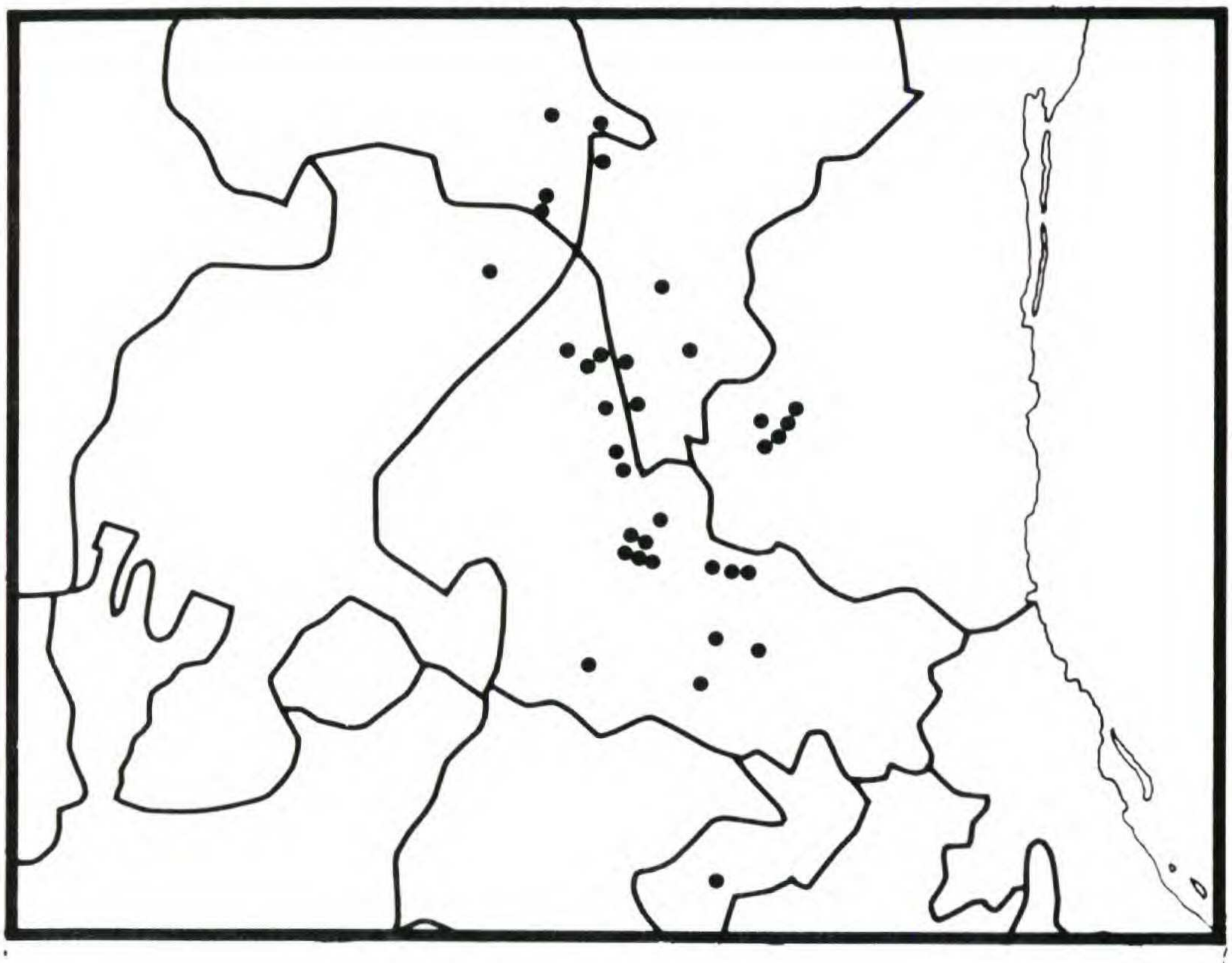

Figure 19. Distribution of *Tiquilia purpusii*.

the Andes. It is also the only species found on both American continents. It is the northernmost species in North America, reaching near the Canadian border in its northern extreme. Considering the broad intracontinental and intercontinental distribution of this species, it is remarkably uniform, the North and South American plants being indistinguishable morphologically.

Tiquilia nuttallii flowers March through September in North America, and November through March in South America.

Tiquilia nuttallii is sometimes confused with *T. palmeri*, with which it grows in the southern limits of its distribution in North America. The two species are most easily distinguished by the characters presented in the accompanying key.

11. **Tiquilia plicata** (Torrey) A. Richardson, Sida **6:** 237. 1976.

Tiquilia brevifolia var. *plicata* Torrey, *In* United States and Mexican Boundary Survey **2:** 136. 1859. TYPE: **California:** Desert west of the Colorado, 28 Nov. 1846, *Lt. Emory s.n.* (Holotype, NY! Photograph, GH!).

Coldenia plicata (Torrey) Coville. Contr. U. S. Nat. Herb. **4:** 163. 1895.

Procumbent or spreading, forming mounds to 6.0 dm. across and 1.5 dm. tall, producing new shoots from underground rhizomes; caudices to 3.0 mm. thick; older stems woody with light brown bark; young branches with fine antrorsely appressed and spreading hairs to 0.7 mm. long. Leaves (Figure 6K) in nodal or apical clusters; blades green, obovate to ovate, 4.5–13.6 mm. long, 2.5–8.0 mm. broad, deeply plicate, 4–7 pairs of crowded lateral veins; upper surfaces with fine appressed hairs converging on the medians between the veins and flowing toward the margins, hairs along margins antrorsely appressed, also with scattered bristles to 0.6 mm. long with thickened mineralized bases; lower surfaces with fine dense spreading and inclined hairs to 0.4 mm. long; petioles filiform, 2.5–11.0 mm. long, with dense antrorsely inclined hairs to 0.7 mm. long. Flower clusters ebracteate. Calyces 2.5–3.0 mm. long, outer and inner surfaces with ascending hairs to 1.0 mm. long, very dense on lower half of inner surfaces; lobes subulate, free nearly to the base. Corollas white, pink, blue, violet, or purple, often with yellow throats, the throats sometimes apically constricted, 3.5–6.0 mm. long; the buds glabrous or glandular. Stamens adnate to the corolla tubes ca. 2/7 the length from base to limb, the veins below stamen attachments often faintly winged or with scales near base of tube. Styles 2.2–3.0 mm. long, cleft 1/2–4/5 the length, attached to the nutlets sub-basally, 0.2–0.3 mm. above the base, exserted beyond the calyces. Nutlets (Figure 9K) 3–4, ovoid to broadly ovoid, 0.8–1.0 mm. long, 0.5–0.7 mm. across, smooth, black and shiny. Chromosome number, $n = 8$.

DISTRIBUTION: Eastern Arizona, southern California, southern Nevada, and adjacent Baja California and Sonora (Figure 22). *Tiquilia plicata* is usually found in desert or beach sands or sandy gravel, from 71 meters below sea level to 770 meters above sea level with associations of *Ambrosia, Atriplex, Baccharis, Cercidium, Ephedra, Larrea, Opuntia, Populus,* and *Prosopis.* It grows in mixed populations with *T. palmeri* and is geographically sympatric with *T. canescens, T. cuspidata, T. latior,* and *T. nuttallii.*

This species flowers February through December.

Tiquilia plicata is the only species known to have underground rhizomes. It is recognized easily by its deeply plicate leaves with 4–7 pairs of lateral veins, and its smooth and shiny black ovoid nutlets with sub-basal style attachment.

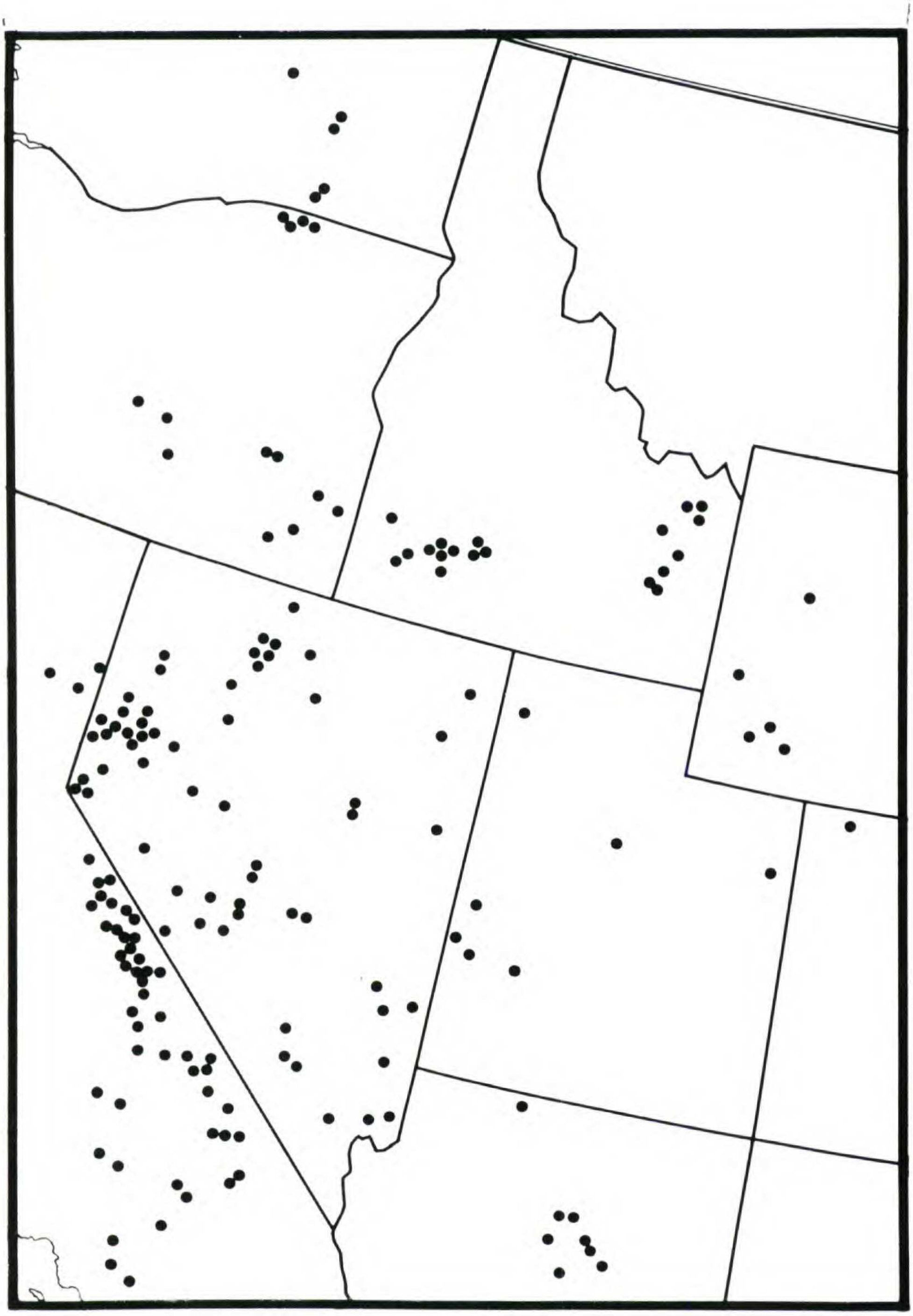

Figure 20. Distribution of *Tiquilia nuttallii*, North America.

12. **Tiquilia cuspidata** (I. M. Johnston) A. Richardson, Sida **6:** 236. 1976.

Coldenia cuspidata I. M. Johnston, Proc. Calif. Acad. IV. **12:** 1137–1140. 1924. TYPE: **Mexico:** In gypsum soil on San Marcos Island, Gulf of California, 12 May 1921, *Johnston 3617* (Holotype, CAS! Isotypes, GH! NY! UC! US!).

Coldenia loretensis M. E. Jones, Contr. W. Bot. **18:** 65. 1933. TYPE: **Mexico:** Baja California. Mts. east of Loreto, 17 Oct. 1930, *Jones 27394* (Holotype, POM! Isotypes, GH! NY! RSA! UC! US!).

Procumbent or spreading, forming mounds to 6.0 dm. across and 2.0 dm. tall; caudices to 10.0 mm. thick; older stems woody with gray to light brown bark; young stems villous or with spreading hairs to 0.5 mm., sometimes hoary. Leaves (Figure 6L) in clusters on short branches or stem apices; blades green to cinereous, ovate, the apex acute with a pungent bristle, 3.5–6.0 mm. long, 1.7–4.0 mm. broad; upper surfaces sparsely to densely pubescent with antrorsely appressed or inclined hairs to 0.4 mm. long, some thicker with mineralized bases, usually more dense basally; lower surfaces with spreading or antrorsely inclined hairs to 0.4 mm. long with thickened mineralized bases especially along veins and margins; petioles ovate-trullate, sometimes filiform distally, 1.5–4.0 mm. long; abaxial surfaces of basal portions with spreading or inclined stiff hairs to 0.5 mm. long, the margins densely ciliate giving a white cottony appearance to the basal portion of lower surfaces of leaf clusters; filiform portions, when present, with spreading bristles to 1.0 mm. long. Flower clusters bracteate. Calyces ca. 2.0 mm. long, with stiff spreading or inclined hairs to 0.5 mm. long; lobes narrowly triangular, free half the length or slightly less, inner surfaces lined with antrorsely appressed hairs. Corollas white tinged bluish or lilac, the throats yellowish green, 3.5–7.0 mm. long; the buds villulose. Stamens adnate to the corolla tubes ca. 2/5 the length from base to limb, the veins below stamen attachments faintly winged most of the length. Styles 1.8–2.5 mm. long, cleft 2/5–3/4 the length, exserted beyond the calyces; attached basally and adnate to the nutlets ca. 3/4 the length, this portion at maturity visible only as a membranous tissue on the nutlet (style lengths given do not include the adnate portion). Mericarps usually 1, sometimes 2, rarely 4. Nutlets (Figure 9L) 1, rarely 2 with the remaining ovules absent or aborting, black and granular; ovate 1.1–1.4 mm. long, 0.7–0.9 mm. broad, attachment scars tapering from 0.3 mm. across at the base to a point ca. 0.4 mm. below the apex. Chromosome number, $n = 8$.

DISTRIBUTION: Mexico, mainly Baja California, also Sonora (Figure 23). *Tiquilia cuspidata* is usually found in sandy desert habitat, often near the Gulf of California, and has been collected in gypseous soils. It grows with *Beloperone californica, Cercidium microphyllum, Cereus giganteus, Dalea emoryi,* and species of *Ferocactus, Fouquieria, Jatropha, Larrea, Lycium, Pachycereus* and *Prosopis.* It is geographically sympatric with *T. palmeri* and *T. plicata,* but has not been reported growing with either of these.

Flowering seasons are January through May and August through November.

Tiquilia cuspidata, with its ovate-trullate petioles, ovate-acute leaf blades, and black granular nutlets with basal style attachments cannot be readily confused with any other North American species of *Tiquilia.* An outstanding character not seen in any other member of the genus is the reduction in number of mericarps. Number of nutlets is further reduced by abortion. Abortion of mericarps, although not uncommon, is a consistent condition in only a few species.

Similarities of nutlet characteristics with those of some species in section *Galapagoa* are considered parallel evolution resulting from selection in similar habitats.

13. **Tiquilia palmeri** (A. Gray) A. Richardson, Sida **6:** 236. 1976.

Coldenia palmeri Gray, Proc. Am. Acad. **8:** 292. 1870. TYPE: **SE California** or **Arizona,** on the lower Colorado, 1869, *Palmer s.n.* (Holotype, GH! Fragment of holotype, fragment #1, UC! Probable isotype, US! Possible isotypes, NY! US!).

Coldenia brevicalyx Watson, Proc. Am. Acad. **24:** 62. 1889. TYPE: On the lower Colorado, 1869, *Palmer s.n.* (Holotype, GH! Fragment of holotype, fragment #1, UC! Probable isotype, US! Possible isotypes, NY! US!).

Coldenia angelica Watson, Proc. Am. Acad. **24:** 62, 63. 1889. TYPE: **Mexico:** BAJA CALIFORNIA. Los Angeles Bay, Gulf of California, 1887, *Palmer 517* (Holotype, US! Isotypes, ARIZ! GH! NY! NY! UC! US!).

Nama coldenioides M. E. Jones, Contr. W. Bot. **12:** 57. 1908. TYPE: **California:** SAN BERNARDINO CO. Needles, 10 May 1884, *Jones 3869* (Holotype, POM!).

Triquiliopsis palmeri (Gray) Rydb., Fl. Rocky Mountains and Adjacent Plains. New York. p. 711, 1917.

Procumbent or spreading, forming mounds to 9.0 dm. across, caudices to 1.4 cm. thick; older stems woody, bark whitish; young stems densely villous or with mostly antrorsely appressed or inclined hairs to 0.6 mm. long. Leaves (Figure 6M) in clusters or unequal pairs at the nodes and in apical clusters; blades gray-green to gray, ovate to suborbicular, sometimes elliptic in Sonora and

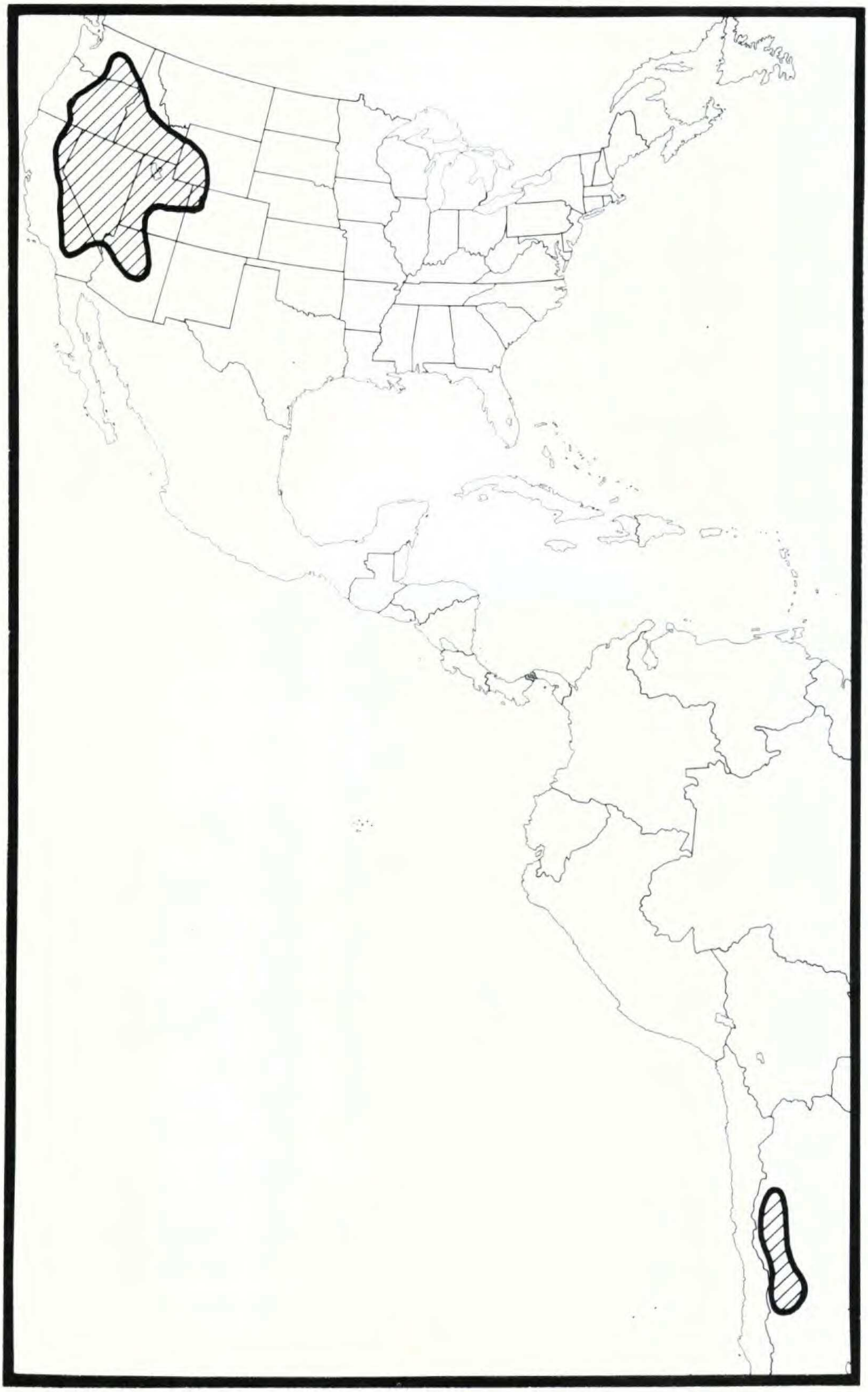

Figure 21. Distribution of *Tiquilia nuttallii*, North and South America.

Baja California, 3.0–14.5 mm. long, 2.5–9.5 mm. broad, with 2–3 pairs of lateral veins ascending at ca. 45° from the midvein, often plicate, margins often irregular; upper surfaces marginally or antrorsely appressed pubescent, hairs to 0.4 mm. long, with scattered spreading or inclined bristles, especially along the margins, to 1.0 mm. long; lower surfaces densely appressed, rarely spreading pubescent; petioles filiform, 2.0–16.0 mm. long, with appressed or spreading hairs to 0.6 mm. long. Flower clusters bracteate. Calyces 2.0–3.5 mm. long, lower half of outer surface with dense spreading or appressed hairs to 0.6 mm. long, upper half less densely pubescent with shorter hairs; lobes narrowly triangular, each with an apical bristle, free ca. half the length, inner surfaces with fine antrorsely appressed hairs. Corollas blue, lavender or purple, with yellow throats, 3.5–9.5 mm. long; the buds hispidulous or glandular. Stamens adnate to the corolla tubes ca. 2/5 the length from base to limb, the veins from the points of stamen attachment winged about half the distance to base of tubes. Styles 2.0–3.0 mm. long, cleft ca. half the length, exserted beyond the calyx lobes, attached to the nutlets basally. Nutlets (Figure 9M) 4, spheroid, 1.0–1.1 mm. across, smooth, brown and shiny, rarely black and minutely aculeate, attachment scars circular. Chromosome numbers, $n = 8$, and aneuploids $n = 9$.

Watson (1889) described *Coldenia brevicalyx* in an attempt to clarify a mixed collection of the holotype of *C. palmeri* Gray, assigning this new name to the entire mounted portion and most of the loose material in a packet on Gray's holotype. He assigned the name *palmeri* to a few loose leaves (actually from *Tiquilia plicata*), which were included in the packet of loose material. Gray (1870) believed these leaves to be from younger plants of the species he described. As stated by Johnston (1924a), it is unrealistic to believe Gray described the few loose leaves as *Coldenia palmeri* and ignored the bulk of the material. Thus, *C. brevicalyx* is an unnecessary renaming of *C. palmeri*.

DISTRIBUTION: Eastern Arizona, southern California, and southern Nevada, and adjacent Baja California and Sonora (Figure 24). *Tiquilia palmeri* is usually found in desert sands or in sand mixed with clay or gravel, from sea level to about 925 meters altitude with associations of *Agave, Ambrosia, Cercidium, Fouquieria, Ja-*

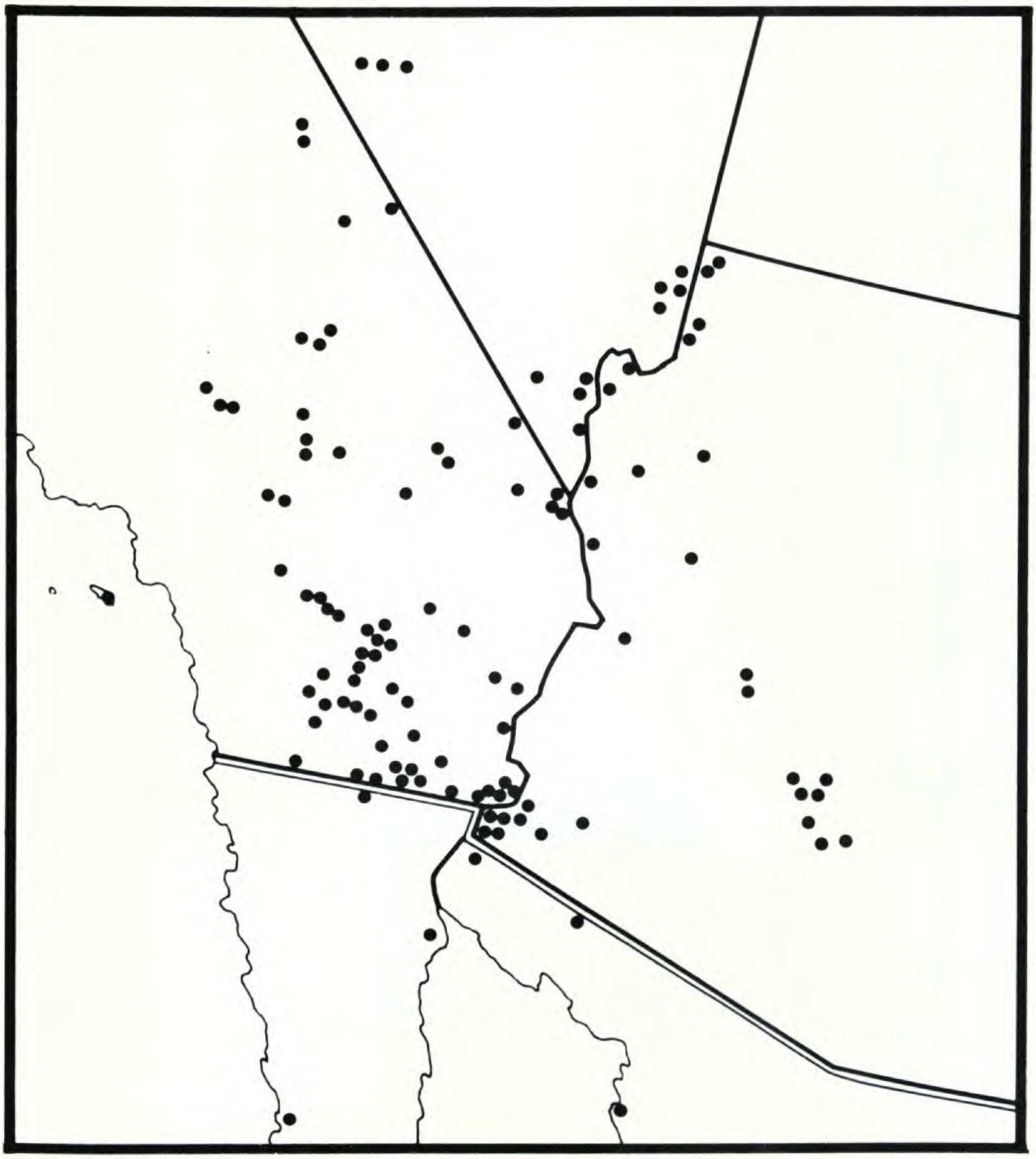

Figure 22. Distribution of *Tiquilia plicata.*

tropha, Larrea, Nicotiana, and *Prosopis.* It grows with *T. plicata* and is geographically sympatric with *T. canescens, T. cuspidata, T. latior,* and *T. nuttallii.*

This species flowers every month of the year, but in any fixed locality the period of active growth is limited.

Tiquilia palmeri is vegetatively similar to *T. nuttallii,* but is quite distinct from that species. The two species are compared in the discussion of *T. nuttallii.*

Tiquilia palmeri, with its spheroid nutlets and gynobasic styles, is reminiscent of the South American sect. *Sphaerocarya,* in particular, *T. conspicua,* the only member of that section with a gynobasic style. This situation must be considered a matter of parallel evolution in similar habitats.

Tiquilia sect. **Tiquilia.** TYPE SPECIES: *Tiquilia dichotoma* (Ruiz & Pavon) Persoon.

Procumbent or semi-erect, herbaceous to suffrutescent, forming mats or mounds. Leaves solitary at the nodes or in clusters on short branches or stem apices; blades narrowly ovate, ovate, or lanceolate, the margins entire or crenate; petioles linear or filiform. Flowers in clusters with the leaves or solitary at the nodes. Calyces persistent or deciduous. Corollas persistent, with invaginations forming prominent ridges below the stamen attachments. Stamens equal or unequal, exserted well beyond the corolla limbs (3.0–8.0 mm.), adnate equally or subequally to the corolla tubes. Style attachments apical. Fruits slightly lobed, of 1–4 nutlets. Nutlets more or less hemi-ovoid, the ventral surfaces broadly flattened, the convex dorsal surfaces and sides blotched grey, brown, and black, minutely colliculate. Chromosome number, $n = 16$.

This section includes four species in South America, in northern Chile and Peru.

KEY TO THE SPECIES OF TIQUILIA SECT. TIQUILIA

a. Leaf blade deeply plicate, usually marginally crenate. ..... b.
  b. Nutlet with a knife-like collar surrounding the ventral surface; corolla 8.5–13.0 mm. long. ..... 16. *T. grandiflora.*
  b. Nutlet without a knife-like collar surrounding the ventral surface; corolla 5.0–6.0 mm. long. ..... 14. *T. dichotoma.*
a. Leaf blade not deeply plicate, marginally entire. ..... c.
  c. Nutlet ventral surface markedly narrowed and shortened by inrolling of carpel; corolla 7.5–10.0 mm. long; calyx indurated, retaining the nutlets, deciduous. ..... 17. *T. ferreyrae.*
  c. Nutlet ventral surface slightly narrowed by inrolling of carpel; corolla 4.5–5.5 mm. long; calyx not indurated, opening to release the nutlets, persistent. ..... 15. *T. simulans.*

14. **Tiquilia dichotoma** (Ruiz & Pavon) Persoon, Syn. Pl. **1:** 157. 1805.

Lithospermum dichotomum Ruiz & Pavon, Prodr. et Fl. Peruviana et Chilensis **2:** 5. *t. 111c.* 1799. TYPE: **Peru:** Lima. Sands toward Lurin, vicinity of the

village of Pachacámac, *Ruiz & Pavon 11/6* (Holotype, MA! Probable isotype, OXF).

Coldenia dichotoma (Ruiz & Pavon) Lehm., Plantae E Familiae Asperifoliarum Nuciferae **1:** 9. 1818.

Coldenia pentandra Juss. ex Steud., Nomenclator Bot. 212. 1821, *nomen. superfl.*, based on an unnamed specimen collected by *Dombey* (Probably *Dombey 364* GH!) and described in passing by Jussieu, Gen. Pl. 130. 1789, as a possible congener of *Coldenia*.

Coldenia dombeyana Juss. ex DC., Prodr. Syst. Nat. **9:** 558. 1845, *nomen. superfl.*, based on an unnamed specimen collected by *Dombey* (Probably *Dombey 364* GH!) and described in passing by Jussieu, Gen. Pl. 130. 1789, as a possible congener of *Coldenia*.

Procumbent to semi-erect, forming mats to 20.0 dm. across; caudices to 8.0 mm. thick; older stems woody, bark whitish or brown; young stems with spreading hairs to 0.9 mm. long. Leaf blades (Figure 7A) green, oblong or ovate, 9.0–20.0 mm. long, 4.0–7.0 mm. broad, with 3–6 pairs of plicate lateral veins, the margins crenate; upper surfaces with appressed hairs to 0.3 mm. long converging on the medians between the veins and flowing toward the margins, antrorsely appressed marginally, also with sparse antrorsely inclined bristles to 0.5 mm. long with thickened mineralized bases; lower surfaces with spreading hairs to 0.3 mm. long, especially along the veins; petioles filiform, 4.5–9.5 mm. long with spreading hairs to 1.0 mm. long, abruptly more dense basally. Flower clusters ebracteate. Calyces persistent, 3.5–5.0 mm. long, with antrorsely inclined hairs to 0.6 mm. long, especially along the lobe margins; lobes subulate, free 2/5–1/2 the length, each with 1 or 2 apical bristles to 0.5 mm. long, inner surfaces with sparse antrorsely appressed hairs. Corollas lilac to milk-white color, 5.0–6.0 mm. long; the buds glabrous. Stamens subequal, exserted to 2.0 mm. beyond the limb, adnate to the corolla tubes equally ca. 3/4 the length from base to limb, the veins below stamen attachments winged (sometimes faintly) near the points of attachment. Styles 4.7–6.0 mm. long, cleft 0.4–0.5 mm. (ca. 1/15–1/9 the length). Nutlets (Figure 9N) 2 or 3, blotched gray and brown, hemi-ovoid, (1.4) 1.7–2.0 mm. tall, 1.0–1.5 mm. across, 0.7–1.0 mm. thick. Cotyledons (after germination) elliptical. Chromosome number, $n = 16$.

DISTRIBUTION: Coastal Peru, in departments of Arequipa, Ica, La Libertad, Lambayeque, Lima, and Piura (Figure 25). *Tiquilia dichotoma* is often found growing in shifting sands, growing alone

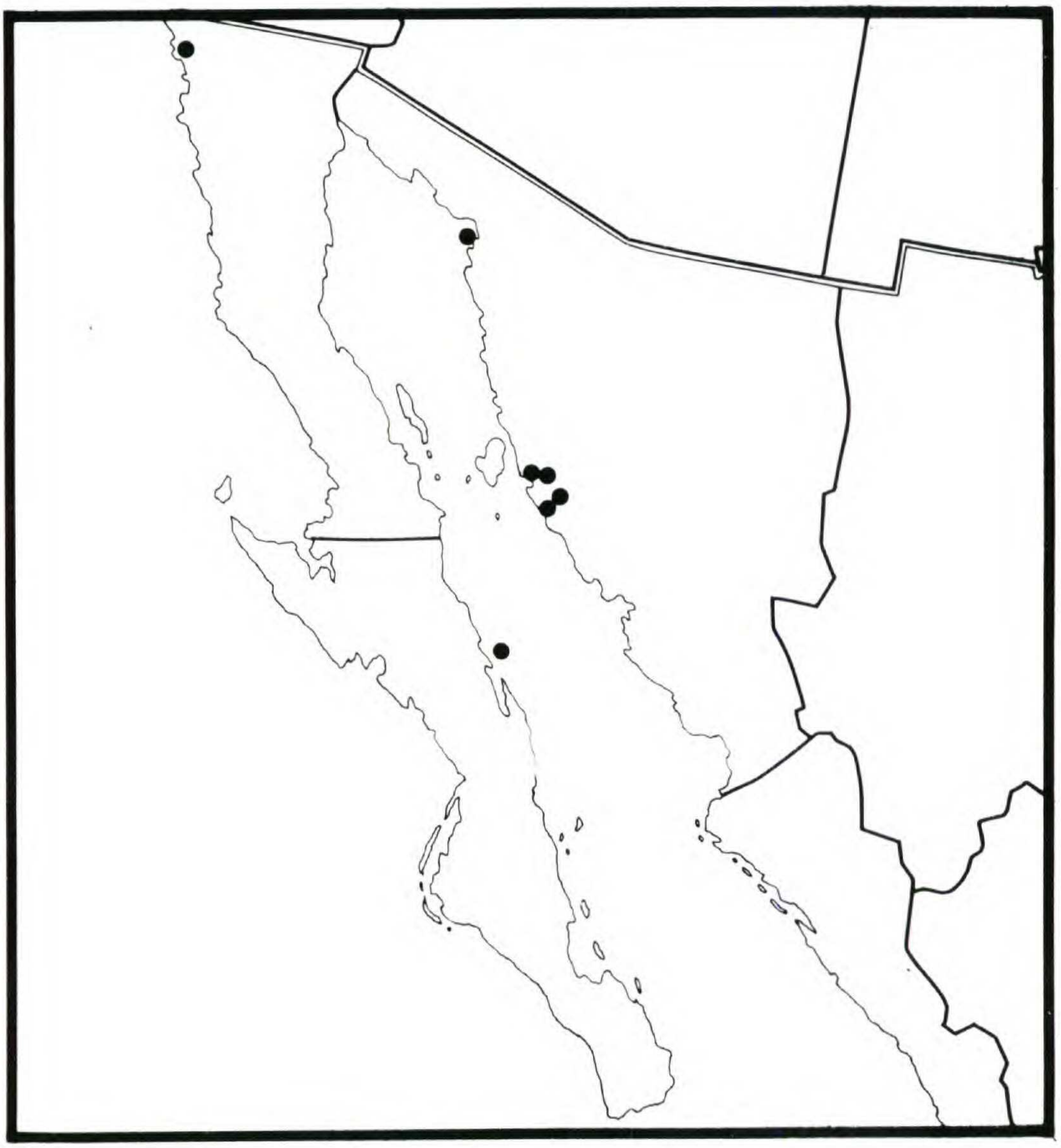

Figure 23. Distribution of *Tiquilia cuspidata*.

or in association with *Alternanthera pubiflora, Baccharis glutinosa, Cristaria multifolia, Galvezia suffruticosa, Grabowskia boerhavifolia,* and *Tribulus terrestris.* It often grows with *T. paronychioides,* and in a population at its southernmost known distribution was found growing with *T. ferreyrae, T. litoralis,* and *T. simulans* as well as *T. paronychioides.* This species is most abundant and most vigorous in northern Peru.

The recorded flowering times are January through June, and August through October.

Tiquilia dichotoma is the type species of the genus. The generic epithet was undoubtedly given in recognition of the vernacular

name, "Tiquil-tiquil," as reported by Ruiz & Pavon (1799), although cited by Persoon (1805) as "Tiquilo."

Two collections vary somewhat from the normal range of morphological characters for the species: *Richardson 2098,* growing with *Tiquilia paronychioides,* and *Richardson 2151A,* growing with *T. ferreyrae, T. litoralis, T. paronychioides,* and *T. simulans.* Since these populations occur in the southern extreme for the species, the slight morphological differences are attributed to environmental effects.

Tiquilia dichotoma is most closely related to *T. simulans.* Johnston (1956) in describing *T. simulans,* suggested the possibility of its being simply a foliar variety of *Tiquilia dichotoma.* Distinguishing and contrasting characters of the two species are listed below.

COMPARISON OF TIQUILIA DICHOTOMA & TIQUILIA SIMULANS

T. dichotoma	*T. simulans*
1. Leaf blades oblong or ovate, 9.0–20.0 mm. long; 3–6 pairs of plicate lateral veins; margins crenate.	1. Leaf blades ovate, 7.5–11.0 mm. long; 2–3 pairs of lateral veins; margins entire.
2. Calyx pubescence more dense along lobe margins.	2. Calyx pubescence more dense apically.
3. Corollas 5.0–6.0 mm. long.	3. Corollas 4.5–5.5 mm. long.
4. Stamens usually subequal.	4. Stamens markedly unequal.
5. Styles 4.7–6.0 mm. long, cleft 1/15–1/9 the length.	5. Styles 4.7–6.0 mm. long, cleft 1/8–1/6 the length.
6. Nutlets hemi-ovoid, the flattened ventral surfaces usually extending the full length and width of the nutlets.	6. Nutlets more or less hemi-ovoid, the flattened ventral surfaces narrowed by inrolling of carpel margins.

15. **Tiquilia simulans** (I. M. Johnston) A. Richardson, Sida **6:** 237. 1976.

Coldenia simulans I. M. Johnston, Jour. Arnold Arb. **37:** 298. 1956. TYPE: **Peru:** AREQUIPA. El Jaguay (sic), km. 538, 22 Aug. 1948, *Scolnik 1010* (Holotype, GH!).

Procumbent or spreading, forming mats or mounds to 12.0 dm. across; caudices to 10.0 mm. thick; older stems woody, bark lurid or sooty colored; young stems with spreading or antrorsely inclined

hairs to 1.0 mm. long. Leaf blades (Figure 7B) green, ovate, 7.5–11.0 mm. long, 3.0–4.0 mm. broad, with 2–3 pairs of lateral veins, the margins entire; upper surfaces with antrorsely closely-appressed hairs to 0.6 mm. long, with few inconspicuous antrorsely appressed bristles to 0.6 mm. long with thickened mineralized bases; lower surfaces with dense antrorsely appressed hairs covering the lateral veins, or less dense and with spreading hairs on the lateral veins; petioles linear, often broader basally, 4.0–5.0 mm. long with spreading hairs to 1.1 mm. long, more dense and longer basally. Flower clusters bracteate. Calyces persistent, ca. 4.5 mm. long, with antrorsely appressed or inclined hairs to 1.0 mm. long, more dense apically; lobes subulate, free ca. 1/2 the length, each with several apical bristles to 0.7 mm. long, inner surfaces with sparse antrorsely appressed hairs. Corollas lilac to sky-blue or milk-white, 4.5–5.5 mm. long; the buds glabrous. Stamens unequal, exserted to 3.0 mm. beyond the limb, adnate to the corolla tubes subequally ca. 2/3 the length from base to limb, the veins below the stamen attachments with thick wings beginning near the points of insertion, becoming membranous below and tapering toward the base. Styles 4.7–6.0 mm. long, cleft 0.6–1.0 mm. (1/8–1/6 the length). Nutlets (Figure 10A) usually 1 or 2, occasionally 3, rarely 4, blotched gray and brown, more or less hemi-ovoid with the minutely colliculate carpel margins curving slightly around the ventral surfaces, 1.6–2.0 mm. tall, 1.1–1.5 mm. across, 0.6–1.1 mm. thick. Chromosome number, $n = 16$.

DISTRIBUTION: *Tiquilia simulans* is known only from the department of Arequipa, Peru, growing in sands at or near the coast, from Puerto Lomas to the lomas south of Atico (Figure 25). It is most abundant at the coast, growing alone or with *T. litoralis* and *T. paronychioides*. In one population about 15 kilometers inland, it grows intermingled with *T. dichotoma, T. ferreyrae, T. litoralis,* and *T. paronychioides*.

The type locality is "El Jahuay" rather than "El Jaguay" as noted on the holotype. Jaguay is located ca. 183 km. south of Lima in the department of Lima, whereas El Jahuay is located ca. 538 km. south of Lima in the department of Arequipa, agreeing with the kilometer notation on the holotype label.

The recorded flowering times are January, April, May, August, and October.

Tiquilia simulans is most closely related to *T. dichotoma.* Contrasting and distinguishing characters are listed in the discussion of that species.

16. **Tiquilia grandiflora** (Phil.) A. Richardson, Sida **6:** 236. 1976.

Coldenia grandiflora Phil., Anales Mus. Nac. Hist. Nat. Chile **2:** 55. 1892. TYPE: **Chile:** Tarapacá. Médanos de Pica, Mar. 1885, *F. Philippi s.n.* (Holotype, SGO 054661! Fragment of holotype, GH! Photograph, NY!).

Procumbent, forming mats to 10.0 dm. across; caudices to 10.0 mm. thick; older stems woody with brown bark; young stems glandular. Leaf blades (Figure 7C) green, narrowly ovate to lanceolate, 11.0–19.0 mm. long, 3.0–5.0 mm. broad, with 3–4 pairs of plicate lateral veins, the margins crenate or entire; upper surfaces with appressed hairs to 0.5 mm. long converging on the medians between the veins and flowing toward the margins, antrorsely appressed marginally, or occasionally all hairs antrorsely appressed; lower surfaces with spreading hairs along the veins and margins; petioles filiform, 6.0–10.0 mm. long, glandular and with sparse bristles to 0.5 mm. long, becoming dense basally. Flower clusters bracteate. Calyces persistent, 5.0–8.0 mm. long, glandular with sparse antrorsely inclined hairs to 0.3 mm. long; lobes narrowly triangular, free ca. 1/2 the length, ciliate, the inner surfaces with dense appressed hairs to 0.6 mm. long. Corollas blue to purple or salmon, with cylindrical tubes, 8.5–13.0 mm. long, without appendages; the buds glandular or glabrous. Stamens subequal, well exserted, up to 8.0 mm. beyond the corolla limb, adnate equally to the corolla tubes ca. 5/6 the length from base to limb, the anthers red. Styles 8.5–13.0 mm. long, cleft 0.5–1.0 mm. (1/20–1/10 the length). Nutlets (Figure 10B) 1–4, usually 1 or 2, blotched gray and brown, hemi-ovoid, 2.4–3.2 mm. tall, 1.1–1.5 mm. across, 0.7–0.9 mm. thick, each with a ventral knife-like collar ca. 0.1 mm. broad apically to 0.4 mm. broad basally. Chromosome number, $n = 16$.

DISTRIBUTION: *Tiquilia grandiflora,* although not abundant, has a rather broad north-south distribution from southern Peru in the department of Arequipa to northern Chile, provinces of Antofagasta, Atacama, and Tarapacá (Figure 26), growing in sand principally at medium altitudes of 1800–2400 meters in the inland deserts, but also at the coast. It is not reported growing with any other plant except *T. elongata.*

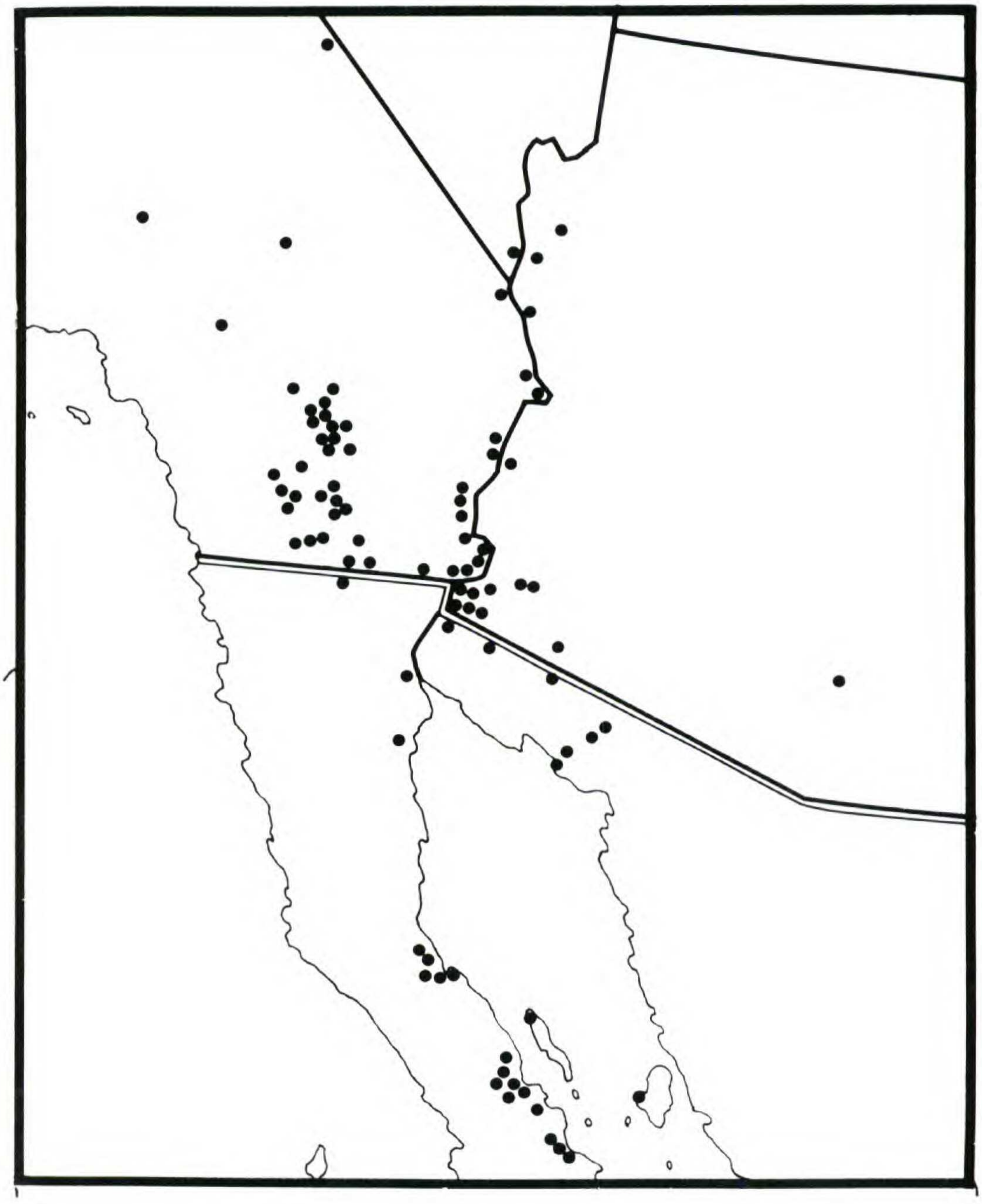

Figure 24. Distribution of *Tiquilia palmeri*.

The recorded flowering times are March, April, October, and November.

Tiquilia grandiflora is most closely related to *T. dichotoma,* but is easily distinguished from that species by its glandular stems and calyces, much larger corollas, and the knife-like ventral collars on the nutlets.

17. **Tiquilia ferreyrae** (I. M. Johnston) A. Richardson, Sida **6:** 236. 1976.

Coldenia ferreyrae I. M. Johnston, Jour. Arnold Arb. **37:** 296–298. 1956. TYPE: **Peru:** AREQUIPA. In sand along highway between Nazca and Chala, km. 545–546, 7 Nov. 1947, *Ferreyra 2506* (Holotype, A!).

Procumbent, forming mats to 11.0 dm. across; caudices to 10.0 mm. thick; older stems woody with lurid bark; young stems with dense spreading or antrorsely inclined hairs to 0.8 mm. long. Leaf blades (Figure 7D) green to gray, ovate to narrowly ovate, 8.5–11.0 mm. long, 4.0–6.0 mm. broad, with 2–3 (rarely 4) pairs of occasionally plicate lateral veins, the margins entire (rarely crenate); upper surfaces with antrorsely appressed hairs to 0.8 mm. long; lower surfaces with spreading hairs along the veins, sometimes with sparse appressed hairs between the veins; petioles filiform, 4.0–6.0 mm. long with spreading hairs to 0.8 mm. long. Calyces deciduous, 5.0–6.5 mm. long, glandular, with spreading or antrorsely inclined hairs to 0.8 mm. long; the basal portion indurated, thickened, deeply sulcate along the lobe sutures, often retaining the nutlets; lobes narrowly triangular, free ca. 1/2 the length, inner surfaces with sparse appressed hairs apically. Corollas white, rarely lilac color, 7.5–10.0 mm. long, the tubes cylindrical, without appendages. Stamens unequal, well exserted, up to 5.0 mm. beyond the corolla limb, adnate equally to the corolla tubes ca. 4/5 the length from base to limb. Styles 10.0–12.8 mm. long, cleft 0.5–0.8 mm. (1/20–1/15 the length). Nutlets (Figure 10C) 1–4, usually 2, blotched gray, brown, and black, ovoid, 1.4–1.7 mm. tall, 1.1–1.4 mm. across, 1.0–1.1 mm. thick, the flattened ventral surfaces ca. 1.4 mm. tall, 0.8 mm. across. Chromosome number, $n = 16$.

DISTRIBUTION: *Tiquilia ferreyrae* is known only from the department of Arequipa, Peru, growing in sands at or near the coast in a limited area from ca. 15 km. NE of Puerto Lomas to ca. 15 km. SE of Camaná (Figure 25). It grows regularly with *T. litoralis,*

and in one population was found growing with *T. dichotoma, T. litoralis, T. paronychioides,* and *T. simulans.*

The recorded flowering times are March through May and October through December.

This well-marked species is most closely related to *Tiquilia simulans* and can be easily distinguished from that species by its larger corollas, nutlets with reduced flattened ventral surfaces, and the deciduous indurated sulcate calyces.

Tiquilia sect. **Sphaerocarya** I. M. Johnston, Contr. Gray Herb. **70:** 57. 1924. TYPE: *Tiquilia litoralis* (Phil.) A. Richardson.

Procumbent or semi-erect, herbaceous to suffrutescent, forming mats or mounds. Leaves solitary at the nodes or in clusters on short branches or stem apices; blades narrowly ovate, ovate, lanceolate, obovate, or narrowly obovate; petioles filiform. Flowers in bracteate clusters with the leaves or solitary at the nodes. Calyces persistent. Corollas deciduous. Stamens included or slightly beyond the corolla limbs, equal or unequal, adnate to the corolla tubes at 3 levels or equally. Style attachments apical, or (*T. conspicua*) gynobasic. Fruits lobed, of 1–4 nutlets. Nutlets spheroid or (*T. atacamensis*) ovate-elliptical, blotched grey, brown, and black, minutely colliculate. Chromosome numbers, $n = 16, 15, \& 14$.

This section includes six species in South America in northern Chile and southern Peru.

KEY TO THE SPECIES OF TIQUILIA SECT. SPHAEROCARYA

a. Nutlet spheroid. ..... b.
b. Leaf margin entire; corolla lilac, sky-blue, or milk-white. ..... c.
c. Corolla 4.5–8.0 mm. long; nutlet without a basal plug from the receptacle; style attachment apical. ..... d.
d. Nutlet with a protruding lip above the attachment scar; stamens exserted, adnate equally to the corolla tube. ..... 19. *T. tacnensis.*
d. Nutlet without a protruding lip above the attachment scar; stamens included or barely exserted, adnate to the corolla tube at three levels. ..... 22. *T. litoralis.*
c. Corolla 7.0–13.5 mm. long; nutlet with a basal plug from the receptacle; style attachment gynobasic. ..... 23. *T. conspicua.*
b. Leaf margin crenate; corolla blue. ..... e.
e. Leaf blade 10.0–23.0 mm. long with 3–4 pairs of lateral veins, upper surface with 2 kinds of hairs; corolla 5.5–12.0 mm. long; longest stamen filament 0.7–1.0 mm. long; nutlet 0.8–0.9 mm. across. ..... 20. *T. elongata.*
e. Leaf blade 5.0–6.0 mm. long with 2–3 pairs of lateral veins, upper surface

with 1 kind of hair; corolla 5.5–6.5 mm. long; longest stamen filament 0.3 mm. long or less; nutlet 0.7–0.8 mm. across. ..... 21. *T. hunteri.*

a. Nutlet ovate in ventral view, elliptical, beaked in lateral view. ..... 18. *T. atacamensis.*

18. **Tiquilia atacamensis** (Phil.) A. Richardson, Sida **6:** 236. 1976.

Coldenia atacamensis Phil., Florula Atacamensis. 211. 1860. TYPE: **Chile:** ANTOFAGASTA. In sand and gravel near San Pedro de Atacama, Jan. 1854, *R. Philippi s.n.* (Holotype, SGO 054649! Fragment of holotype, GH! Photograph of holotype, NY!).

Coldenia parviflora Phil., Anales Mus. Nac. Hist. Nat. Chile **2:** 55. 1892. TYPE: **Chile:** ANTOFAGASTA. Near Socaire, 2 Feb. 1885, *Fr. Philippi s.n.* (Holotype, SGO 054653! Photograph of holotype, NY! Possible isotypes, GH! SGO 042280!).

Procumbent, forming mats to 6.0 dm. across; caudices to 0.5 cm. thick; older stems woody with whitish to lurid colored bark; young stems with antrorsely appressed or sharply inclined straight hairs to 0.5 mm. long. Leaf blades (Figure 7E) gray-green, narrowly ovate to ovate, 5.0–8.0 mm. long, 2.0–4.0 mm. broad, with 2 pairs of plicate lateral veins, the margins entire; upper surfaces with appressed hairs to 0.3 mm. long converging on the medians between the veins and flowing toward the margins, antrorsely inclined or appressed marginally, also with occasional inclined bristles to 0.5 mm. long and 1 or 2 apical bristles to 0.5 mm. long; lower surfaces with appressed and spreading hairs to 0.3 mm. long (leaves on specimens from Pica are larger and have many stiff antrorsely inclined bristles to 0.9 mm. long); petioles expanding near the base, 4.0–7.0 mm. long with spreading hairs to 1.0 mm. long. Calyces 3.5–4.5 mm. long with antrorsely inclined stiff hairs to 0.7 mm. long, more dense along the lobe margins; lobes narrowly triangular, free ca. 1/2 the length, each with 1 or 2 slightly thicker apical hairs to 0.5 mm. long, the inner surfaces with sparse antrorsely appressed hairs. Corollas violet to lilac with yellow to orange throats, the color fading with age, 4.0–5.5 mm. long; the buds villulose and glandular. Stamens unequal, slightly exserted, adnate to the corolla tubes at 3 levels ca. 1/2 the length from base to limb, the veins below the stamen attachments usually winged near the bases. Styles 2.5–5.0 mm. long, cleft 1/6–1/4 the length, exserted beyond the calyces; attached to the nutlets apically. Nutlets (Figure 10D) 4, occasionally less, ovate ventrally, elliptical and beaked laterally, 1.1–1.3 mm. tall, 0.7–1.1 mm. across. Chromosome number not known.

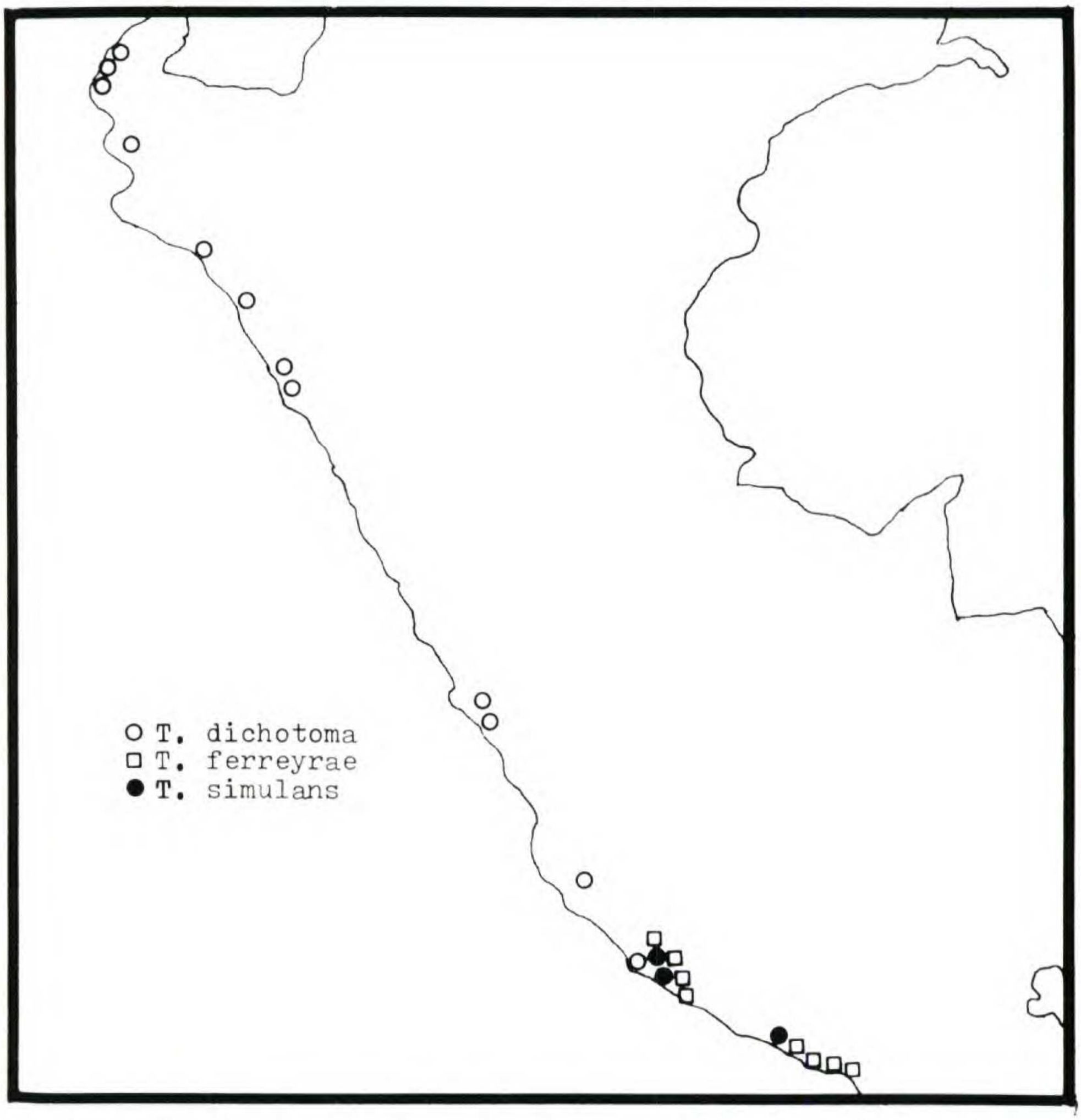

Figure 25. Distribution of *Tiquilia dichotoma*, *T. ferreyrae*, and *T. simulans*.

DISTRIBUTION: Chile, in the provinces of Antofagasta and Tarapacá (Figure 26), mainly in the higher altitude inland deserts at 1400–4100 meters, in sand and gravel. *Tiquilia atacamensis* often grows alone, and is the dominant plant where it occurs. It is extremely abundant near San Pedro de Atacama where large populations covering the hillsides extend for many kilometers. *T. paronychioides* and *Tribulus sp.* sometimes grow in association with this species.

Recorded flowering times are January, February, May, September, and October. More extensive collection of this species would probably reveal a more extended blooming season.

Tiquilia atacamensis is distinct from all other species in the sect. *Sphaerocarya* in having ovate-elliptical, beaked nutlets rather than spheroid nutlets. It is most closely related to *T. tacnensis,* which has similar calyces and general pubescence and a similar flavonoid chromatograph pattern (Richardson, 1975, unpublished). The two species are contrasted below.

COMPARISON OF TIQUILIA ATACAMENSIS & TIQUILIA TACNENSIS

T. atacamensis	*T. tacnensis*
1. Internodes usually thick and short.	1. Internodes usually slender and elongate.
2. Leaves 5.0–8.0 mm. long, 2 pairs of lateral veins.	2. Leaves 4.0–5.5 mm. long, usually 3 pairs of lateral veins.
3. Corollas violet to lilac, appendaged.	3. Corollas sky blue, not appendaged.
4. Stamens slightly exserted.	4. Stamens exserted 1.5–2.5 mm.
5. Nutlets ovate-elliptical, beaked, with smaller collicula.	5. Nutlets spheroid, not beaked, with an apical lip, with larger collicula.

19. **Tiquilia tacnensis** A. Richardson, Sida **6:** 238–240. 1976. TYPE: **Peru:** Tacna. Ca. 10 km. S of Camiara, 70 km. N of Tacna, 13 Apr. 1973, *Richardson 2130* (Holotype, TEX! Isotypes, ARIZ! CAS! F! GH! MICH! NY! POM! UC! US!).

Procumbent, forming mats to 5.0 dm. across; caudices to 10.0 mm. thick; older stems woody with sooty colored bark; young stems with antrorsely appressed or inclined straight hairs to 0.5 mm. long. Leaf blades (Figure 7F) olive green, ovate, 4.5–5.5 mm. long, 3.0–3.5 mm. broad, with usually 3 pairs (occasionally 2 pairs) of plicate lateral veins, the margins entire; upper surfaces with appressed hairs to 0.3 mm. long converging on the medians between the veins and flowing toward the margins, antrorsely appressed marginally, also with occasional inclined bristles to 0.7 mm. long; lower surfaces with dense spreading and appressed straight hairs to 0.5 mm. long, often covering all but the midvein; petioles 3.0–4.0 mm. long with dense antrorsely inclined hairs to 0.8 mm. long. Calyces ca. 3.5 mm. long with antrorsely inclined

stiff hairs to 1.0 mm. long, more dense along the margins; lobes narrowly triangular, free ca. 1/2 the length, each with 1 or 2 slightly thicker apical hairs to 0.5 mm. long, the inner surfaces with sparse appressed hairs. Corollas sky blue with yellow throats, 5.0–6.0 mm. long; the buds glandular. Stamens subequal, exserted 1.5–2.5 mm. beyond the limb, adnate to the corolla tubes equally ca. 1/2 the length from base to limb, the veins below stamen attachments not appendaged. Styles 5.5–5.6 mm. long, cleft 1/9–1/5 the length, exserted beyond the calyces; attached to the nutlets apically. Nutlets (Figure 10E) 4, occasionally less, colliculate, spheroid with a protruding lip above the attachment scar, 1.0–1.1 mm. tall, 0.9–1.2 mm. across. Chromosome number, $n = 16$.

DISTRIBUTION: Peru, southern Tacna near the Chilean border (Figure 27). One large uniform population is known. Extending for ca. 30 kilometers, it is the dominant plant growing in sand with *Argelia feullei, Nolana sp.*, and various grasses.

This species is known to flower in November and April.

The specific epithet was given in recognition of the department of Tacna, Peru, to which the species is endemic.

Tiquilia tacnensis appears to be most closely related to *T. atacamensis*, having a similar flavonoid chromatograph pattern (Richardson, 1975, unpublished), and similar calyces and general pubescence. The two species are contrasted in the discussion of *T. atacamensis*.

Tiquilia tacnensis is also closely related to *T. litoralis*, differing in flavonoid chromatograph pattern, chromosome number of $n = 16$, leaf blades with usually 3 pairs of lateral veins, paucity or absence of long stiff bristles on the calyces, and the nutlets with a protruding lip above the attachment scar and with slightly larger collicula. There are also some similarities to *T. elongata* and *T. hunteri*.

20. **Tiquilia elongata** (Rusby) A. Richardson, Sida **6:** 236. 1976.

Coldenia elongata Rusby, Description of Three Hundred New Species of South American Plants. Rusby. New York. p. 107. 1920. TYPE: **Peru:** AREQUIPA. Dry hillsides, Yura, 10 Aug. 1901, *Williams 2562* (Holotype, NY! Isotype, NY! Fragment and photograph of isotype, GH!).

Procumbent or semi-erect subshrubs forming mounds to 1 meter across; caudices to 10.0 mm. thick; older stems with light brown or

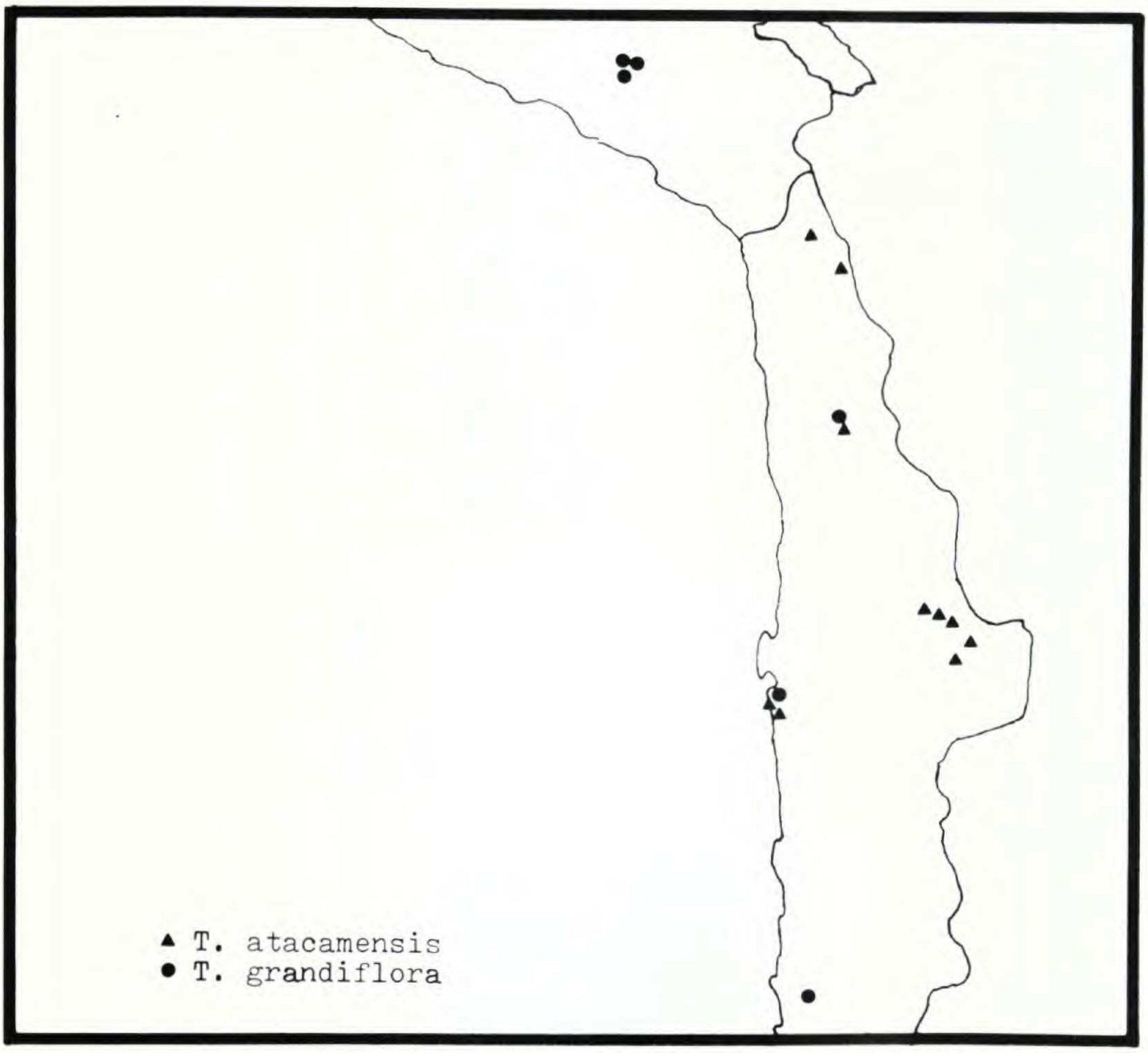

Figure 26. Distribution of *Tiquilia atacamensis* and *T. grandiflora.*

whitish bark; young stems with dense spreading or antrorsely inclined straight hairs to 1.2 mm. long, sometimes hoary. Leaf blades (Figure 7G) narrowly ovate to lanceolate or narrowly obovate, 10.0–23.0 mm. long, 3.0–10.0 mm. broad, the margins crenate, 3–4 pairs of usually plicate lateral veins running to the sinuses; upper surfaces with antrorsely appressed or inclined hairs to 0.4 mm. long and scattered thicker hairs to 0.9 mm. long with thickened mineralized bases; lower surfaces with dense spreading hairs especially along the veins; petioles 6.0–16.0 mm. long with dense spreading hairs to 1.0 mm. long. Calyces 4.0–5.5 mm. long with antrorsely inclined stiff hairs to 1.5 mm. long; lobes linear to narrowly triangular, free ca. 4/5 the length, each with 1 or few apical bristles to 0.7 mm. long, ciliate with hairs to 0.8 mm. long, inner surfaces with sparse antrorsely appressed hairs. Corollas blue, sometimes

constricted at the throat, 5.5–12.0 mm. long; the buds villulose. Stamens unequal, included; filaments to 1.0 mm. long, adnate to the corolla tubes at 3 levels ca. 3/7 the length from base to limb, the veins below the stamen attachments usually winged. Styles 4.0–6.2 mm. long, cleft 1/5–1/4 the length, attached to the nutlets apically. Nutlets (Figure 10F) 4, sometimes less, spheroid, 0.8–0.9 mm. across. Chromosome number, $n = 16$.

DISTRIBUTION: *Tiquilia elongata* is limited almost entirely to the inland desert in southern Peru, department of Arequipa, growing in sand, sandy clay, and volcanic ash (Figure 28). It is most abundant around Arequipa and Yura. One collection (*Richardson 2129*) was made from a few plants growing near the coast in Peru's southernmost department, Tacna. This species is usually dominant where it occurs, growing alone or with species of *Encelia, Franseria,* and various cacti. It grows with *T. grandiflora* and *T. paronychioides.*

Flowering seasons are January through April, June through August, October, and November.

A vernacular name for this plant is "Paco-paco."

Tiquilia elongata is easily distinguished from the other species of sect. *Sphaerocarya* that have apical styles and spheroid nutlets by its blue corollas and large crenate leaves with two kinds of hairs on the upper surface. It is also fairly well separated geographically from these species.

21. **Tiquilia hunteri** A. Richardson, Sida **6:** 238, 239. 1976. TYPE: **Peru:** AREQUIPA. Km. 714 S of Lima, between Chala and Camaná, 8 Apr. 1973, *Richardson 2106* (Holotype, TEX! Isotypes, CAS! F! GH! UC! US!).

Semi-erect subshrubs with internodes to 2.0 cm. long, forming mounds to 4.0 dm. across; caudices to 5.0 mm. thick; older stems with whitish bark; young stems with dense spreading hairs to 1.5 mm. long. Leaf blades (Figure 7H) green, narrowly ovate, 5.0–6.0 mm. long, 2.0–2.5 mm. broad, the margins usually crenate, sometimes entire, 2–3 (rarely 4) pairs of deeply plicate lateral veins running to the sinuses; upper surfaces with antrorsely inclined thick white bristles to 1.1 mm. long with thickened mineralized bases, each blade with a stout apical bristle; lower surfaces with spreading hairs mostly along the veins; petioles 3.0–4.5 mm. long with

spreading hairs to 1.2 mm. long. Calyces ca. 4.0 mm. long with sparse antrorsely inclined hairs to 0.5 mm. long; lobes narrowly triangular, free ca. 3/4 the length, ciliate, each with a stiff apical bristle to 0.8 mm. long, inner surfaces with sparse antrorsely appressed hairs. Corollas blue, sometimes constricted at the throat, 5.5–6.5 mm. long; the buds glandular. Stamens unequal, included, filaments short, to 0.3 mm. long, adnate to the corolla tubes at 3 levels ca. 3/5 the length from base to limb, the veins below stamen attachments lightly winged basally. Styles 4.0–4.5 mm. long, cleft ca. 1/9 the length, exserted beyond the calyces; attached to the nutlets apically. Nutlets (Figure 10G) 4, occasionally less, spheroid, 0.7–0.8 mm. across. Chromosome number, $n = 14$.

DISTRIBUTION: Known only from the type locality (Figure 27). One small, uniform population is known, growing in roadside sands with *Tiquilia litoralis*.

The specific epithet was given in recognition of my friend John H. Hunter (born 1900) of Brownsville, Texas, who has encouraged and aided many students interested in the biological sciences.

Tiquilia hunteri is most closely related to *T. elongata,* from which it is well separated geographically. It is also closely related to *T. litoralis* and *T. tacnensis*.

22. **Tiquilia litoralis** (Phil.) A. Richardson, Sida **6:** 236. 1976.

Coldenia litoralis Phil., Florula Atacamensis. 211. 1860. TYPE: **Chile:** ATACAMA. In littoral sand at Caldera, Dec. 1853, *Philippi s.n.* (Holotype, SGO 042286! Possible isotypes, SGO 054659! GH! Photographs of holotype, GH! NY!).

Coldenia mitis Phil., Anales Univ. Chile **90:** 229. 1895. TYPE: **Chile:** ATACAMA. Desert of Atacama, Quebrada del Rosario, *San Roman s.n.* (Holotype, SGO 054654! Photograph of holotype, NY!).

Coldenia virens Phil., Anales Univ. Chile **90:** 229, 230. 1895. TYPE: **Chile:** ATACAMA. Near Caldera, Sep. 1885, *Philippi s.n.* (Holotype, SGO 054658!).

Procumbent with elongate internodes to 5.0 cm. long, forming mats to 6.0 dm. across; caudices to 10.0 mm. thick; older stems woody with whitish bark; young stems with dense spreading hairs to 1.0 mm. long. Leaf blades (Figure 7I) green to olive-green, ovate, 3.5–8.0 mm. long, 2.5–4.5 mm. broad, with 2–3 pairs of often plicate lateral veins, the margins entire; upper surfaces with inclined or appressed hairs to 0.5 mm. long converging on the medians between the veins and flowing toward the margins, antrorsely inclined or appressed marginally, and with scattered an-

trorsely inclined thick bristles to 1.0 mm. long with thickened mineralized bases (sometimes all hairs antrorsely inclined or appressed); lower surfaces with spreading hairs to 0.8 mm. long, mainly along the veins; petioles 4.0–8.0 mm. long with dense spreading hairs to 1.0 mm. long. Calyces 4.5–5.0 mm. long with antrorsely inclined bristles to 1.0 mm. long; lobes narrowly triangular, free ca. 3/5 the length, each with 1 or 2 apical bristles to 1.0 mm. long, inner surfaces with sparse appressed hairs. Corollas sky-blue to milk-white with yellow throats, 4.5–8.0 mm. long; the buds villulose. Stamens unequal, reaching the limb, the longest ones occasionally slightly exserted; filaments to 17.0 mm. long, adnate to the corolla tubes at 3 levels ca. 3/5 the length from base to limb, the veins below the stamen attachments lightly winged near the bases or without appendages. Styles 3.0–6.3 mm. long, cleft 1/5–1/3 the length, exserted beyond the calyces, attached to the nutlets apically. Nutlets (Figure 10H) 4, occasionally less, spheroid, 0.8–1.1 mm. across. Chromosome number, $n = 15$.

DISTRIBUTION: Chile, in the provinces of Antofagasta, Atacama, and Tarapacá; and Peru, in the departments of Arequipa and Tacna (Figure 28). *Tiquilia litoralis* is almost entirely limited to the littoral sands of these countries and is usually the dominant plant. It grows alone or in association with *Perityle emoryi* and species of *Frankenia, Nolana,* and *Onoseris.* It often grows with *T. ferreyrae* and is occasionally found growing with *T. paronychioides* and *T. simulans.*

Tiquilia litoralis flowers January through May, and August through December.

One specimen, *Richardson 2149,* is difficult to place, having the included stamens and spheroidal nutlets of sect. *Sphaerocarya,* and the persistent corolla, flattened but reduced ventral nutlet surface, and chromatographic profile of *T. simulans* of sect. *Tiquilia.* This collection was made from a single plant growing in a large mixed population of *T. simulans* (*Richardson 2150*) and *T. litoralis* (*Richardson 2151*). Corolla color, plant habit, and vegetative morphology were almost identical to those of the surrounding plants of *T. simulans.* A careful search revealed no additional similar plants, but they could have been overlooked since there were many plants without flowers. In the absence of populational data, this specimen is referred to *T. litoralis.*

Tiquilia litoralis, T. tacnensis, T. elongata, and *T. hunteri* are closely related and have morphological similarities that sometimes make them difficult to distinguish without close examination.

23. **Tiquilia conspicua** (I. M. Johnston) A. Richardson, Sida **6:** 236. 1976.

Coldenia conspicua I. M. Johnston, Jour. Arnold Arb. **16:** 183–185. 1935. TYPE: **Peru:** AREQUIPA. Sand flat at Mejía, 26 Oct. 1923, *Guenther & Buchtien 155* (Holotype, HBG!).

Procumbent, forming mats to 5.0 dm. across, dichotomous branching not conspicuous; caudices to 6.0 mm. thick; older stems somewhat woody, bark sooty colored; young stems with spreading or inclined hairs 1.1–1.5 mm. long. Leaf blades (Figure 8A) green, ovate to elliptical, 7.0–12.0 mm. long, 3.0–5.5 mm. broad, with 2 pairs of lateral veins, the margins narrowly revolute, entire; upper surfaces with antrorsely inclined straight hairs to 1.0 mm. long and thicker bristles to 1.2 mm. long with mineralized bases; lower surfaces with spreading hairs to 1.0 mm. long, especially along margins and veins; petioles 4.5–11.0 mm. long with dense spreading hairs to 1.3 mm. long. Calyces 6.5–10.0 mm. long with spreading and antrorsely inclined hairs 1.0–1.5 mm. long, especially along the lobe margins; lobes narrowly triangular, free nearly to the base, each lobe with 2 or several bristles to 1.0 mm. long at or near the apex, inner surfaces with sparse appressed hairs. Corollas lilac color, 7.0–13.5 mm. long; the buds glandular. Stamens subequal, reaching the limb or barely exserted, adnate to the corolla tubes at 3 levels ca. 7/9 the length from base to limb, the veins below the stamen attachments unilaterally winged from about the middle of the tube, tapering near the base. Styles 5.5–9.3 mm. long, cleft ca. 1/6 the length, exserted beyond the calyces; attached basally to a gynobase. Nutlets (Figure 10I) 4, spheroid, 1.0–1.5 mm. across, each nutlet with a basal plug, leaving a cupulate gynobase when falling away. Chromosome number, $n = 16$.

DISTRIBUTION: Peru, in the department of Arequipa, growing in sands mainly along the coast but also at the higher altitudes of Estación Cachendo and Yura (Figure 27). This species has not been reported to be growing with any other plants.

Reported flowering times are April, August, October, and November. More extensive collecting would probably reveal a longer blooming period.

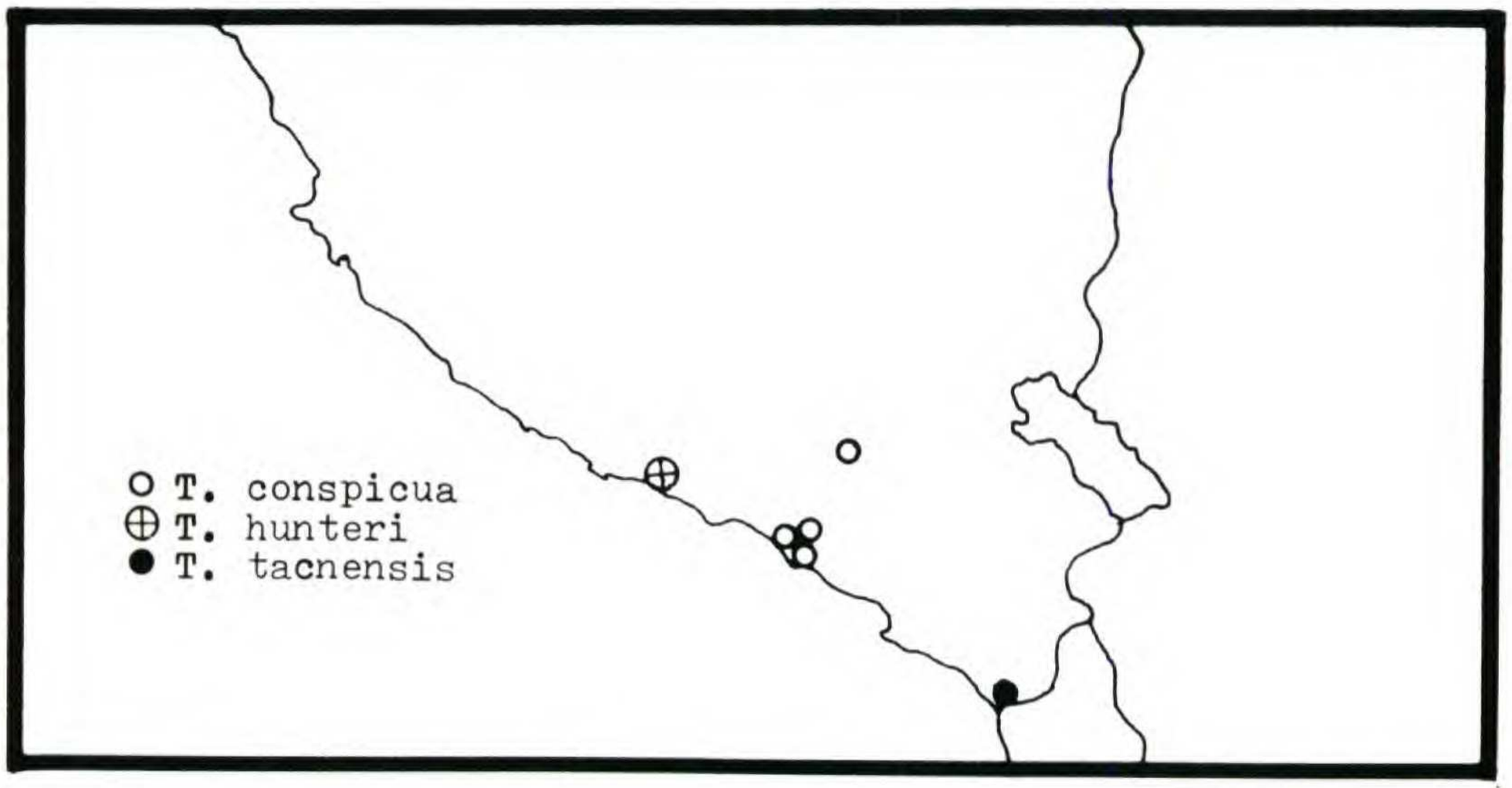

Figure 27. Distribution of *Tiquilia conspicua, T. hunteri,* and *T. tacnensis.*

Tiquilia conspicua differs from other species of the sect. *Sphaerocarya* in having much larger floral parts and nutlets, in its narrowly revolute leaf margins, and its gynobasic style.

One collection, *Mexia 4178,* is in question. This collection consists entirely of small seedlings with flowers but without mature nutlets. The floral parts are much smaller than those of the mature plants examined, but the leaf characters and collection locality fit *Tiquilia conspicua.* Therefore it is referred to this species.

Tiquilia sect. **Galapagoa** A. Richardson. TYPE: *Tiquilia darwinii* (Hooker f.) A. Richardson.

Procumbent or semi-erect, herbaceous to suffrutescent, forming mats or mounds. Leaves solitary at the nodes or in clusters on short branches or stem apices; blades ovate to elliptical, lanceolate, obovate, or narrowly obovate; on plants which have been subjected to long dry periods, blades tend to recurve, giving a convex upper surface and a narrowly ovate to obovate shape; petioles ovate-trullate. Flowers solitary and axillary, or in clusters with the leaves. Calyces deciduous or persistent. Corollas deciduous. Stamens included or slightly beyond the corolla limbs, equal or unequal, adnate to the corolla tubes equally or at 3 levels. Fruits lobed, of 4 nutlets. Nutlets ovoid, black, smooth, granular, or minutely colliculate.

This section includes four species in South America, three of them endemic to the Galapagos Islands, and one widespread species in Chile, Ecuador, and Peru.

KEY TO THE SPECIES OF TIQUILIA SECT. GALAPAGOA

a. Nutlet granular or minutely colliculate, dull. ..... b.
  b. Nutlet 0.7–1.2 mm. tall, attachment scar width constant the full length; calyx lobes narrowly triangular. ..... 24. *T. paronychioides.*
  b. Nutlet 0.6–1.0 mm. tall, attachment scar widening at apex and base; calyx lobes narrowly ovate. ..... 25. *T. galapagoa.*
a. Nutlet smooth, shiny. ..... c.
  c. Nutlet deeper dorsi-ventrally than broad; leaf blade 2.3–4.0 mm. long, lower surface with spreading and antrorsely inclined and appressed hairs along the midrib; corolla 2.5–3.0 mm. long, without appendages; stamens included. ..... 26. *T. nesiotica.*
  c. Nutlet more or less the same dimension dorsi-ventrally as broad; leaf blade 2.0–2.7 mm. long, lower surface with antrorsely appressed hairs, none spreading or pointing away from the apex; corolla 1.3–1.7 mm. long with small, unialate wings below the stamen attachments; stamens extending to limb or slightly beyond. ..... 27. *T. darwinii.*

24. **Tiquilia paronychioides** (Phil.) A. Richardson, Sida **6:** 236. 1976.

Coldenia paronychioides Phil., Anales Mus. Nac. Hist. Nat. Chile **2:** 55. 1892. TYPE: **Chile:** TARAPACÁ. Pampa Tamarugal, Mar. 1884, *F. Philippi s.n.* (Holotype, SGO 054652! Fragment of holotype, GH! Probable isotype, SGO 042277!).

Coldenia tenuis Phil., Anales Mus. Nac. Hist. Nat. Chile **2:** 55. 1892. TYPE: **Chile:** TARAPACÁ. Tambillo Chico, Mar. 1885, *Rahmer s.n.* (Holotype, SGO 042279! Fragment of holotype, GH! Probable isotype, US! Photograph of US probable isotype, NY!).

Coldenia aggregata Rusby, Description of Three Hundred New Species of South American Plants. Rusby. New York. pp. 106, 107. 1920. TYPE: **Peru:** PIURA. Paita, 25 Jul. 1901, *Williams 2913* (Holotype, NY! Fragment of holotype, GH!).

Procumbent, occasionally semi-erect, forming mats to 21.0 dm. across; caudices to 10.0 mm. thick; older stems woody with brown bark; young stems with dense appressed or antrorsely inclined hairs to 0.8 mm. long. Leaf blades (Figure 8B) green to gray-green, narrowly obovate to lanceolate or obovate, 3.0–6.0 mm. long, 1.2–3.0 mm. broad, marginally entire; upper surfaces with antrorsely appressed hairs to 0.3 mm. long, and sparse or dense antrorsely inclined bristles to 1.0 mm. long, midrib plicate, lateral veins usually indistinct; lower surfaces with spreading hairs to 0.3 mm. long along the prominent midrib; petioles trullate, sometimes filiform distally,

0.5–5.0 mm. long with dense spreading hairs to 0.8 mm. long. Flowers axillary and solitary, and in ebracteate clusters with the leaves. Calyces deciduous, 2.5–3.5 mm. long with antrorsely inclined or appressed hairs to 1.0 mm. long; lobes narrowly triangular, free 1/3–1/2 the length, ciliate. Corollas white to milk-white, 1.7–4.0 mm. long, the tubes usually cylindrical, without appendages; the buds glabrous. Stamens unequal, included, adnate to the corolla tubes at 3 levels 1/3–1/2 the length from base to limb. Styles 0.7–2.0 mm. long, cleft 1/5–1/3 the length (0.2–0.9 mm.), attached apically or sub-apically to the nutlets. Nutlets (Figure 10J) black, granular, usually unequal in size within a fruit, 0.7–1.2 mm. tall, 0.4–0.7 mm. broad; the attachment scars to 0.2 mm. broad, ca. 0.9 mm. long, not enlarged apically or basally. Cotyledons (after germination) elliptical. Chromosome number, not known.

DISTRIBUTION: *Tiquilia paronychioides* is mainly coastal, from central Ecuador through Peru to northern Chile, occurring also inland around Arequipa, Peru, and in Chile (Figure 29). One collection was made in La Paz, Bolivia, and one in Panama. This species grows in sand or sandy clay in association with *Alternanthera pubiflora, Baccharis glutinosa, Cristaria multiflora, Galvezia suffruticosa, Tribulus terrestris*, species of *Cordia* and *Ipomea*, and various cacti and grasses. It grows with *T. atacamensis, T. dichotoma, T. elongata, T. ferreyrae, T. litoralis*, and *T. simulans*, and is the only species of *Tiquilia* in South America which successfully competes to any degree with other plants.

This species flowers January through December.

Tiquilia paronychioides is known as "flor de arena" and "yerba blanca." It is sometimes used to treat gonorrhea (*Stork, et al. 9197*, GH).

Tiquilia paronychioides varies in leaf morphology. In seedlings, the margins are often not revolute; in older plants which have been receiving copious amounts of water, the blades are often proportionately broader with only slightly revolute margins, and less densely pubescent. The number of bristles present is extremely variable, but fairly consistent within a given population.

In northern Peru and Ecuador, which receive greater amounts of rain than regions farther south, plants are often found with proportionately larger leaves and stems.

There are no closely related species on the mainland of South

America. *Tiquilia paronychioides* is distinct with its smaller leaves and corollas and its smaller, black, ovoid nutlets lacking a broad ventral surface. The species of the Galapagos Islands are the most closely related taxa.

25. **Tiquilia galapagoa** (J. T. Howell) A. Richardson, comb. nov.
Coldenia galapagoa J. T. Howell, Proc. Calif. Acad IV. **12:** 108, 109. 1937. TYPE: **Ecuador:** GALAPAGOS ISLANDS. Conway Bay, Indefatigable Island, 8 Jun. 1932, *Howell 9862* CAS! (Isotypes, CAS! GH!).

Prostrate or somewhat ascending, cinereous, forming mats to 8.0 dm. across; caudices to 10.0 mm. thick; older stems woody with whitish bark; young stems with dense antrorsely appressed and inclined or spreading hairs to 0.7 mm. long. Leaf blades (Figure 8C) suborbicular to ovate or lanceolate, 2.0–5.0 mm. long, 1.5–3.5 mm. broad, marginally entire; upper surfaces with antrorsely appressed or inclined hairs to 0.9 mm. long with thickened mineralized bases, midrib plicate, lateral veins moderately so or indistinct; lower surfaces with spreading hairs along the midribs and lateral veins, or completely covered with antrorsely and marginally appressed hairs; petioles trullate to rectangular, 1.0–2.5 mm. long, ciliate, the abaxial surface with antrorsely appressed hairs or occasionally glabrate. Flowers axillary and solitary, also in small ebracteate groups of 2 or 3 with the leaf clusters. Calyces persistent, 1.5–2.5 mm. long, with dense antrorsely inclined hairs to 1.0 mm. long, becoming less dense apically; lobes 5, subequal, narrowly ovate, free ca. 1/2 the length, usually spreading at maturity; the fused bases with 4 cups enclosing the nutlets. Corollas whitish or white with purple, 1.1–2.8 (3.5) mm. long, without appendages; the buds villous. Stamens subequal, included, adnate equally to the corolla tubes ca. 1/3 the length from base to limb. Styles 1.0–2.3 mm. long, cleft 0.7–2.1 mm. or to the base, attached apically to the nutlets. Nutlets (Figure 10K) brown or black, dull, minutely colliculate, 0.6–1.0 mm. tall, 0.4–0.5 mm. broad, the attachment scar nearly the full length, enlarging slightly apically and basally. Cotyledons (after germination) elliptical. Chromosome number, not known.

DISTRIBUTION: Galapagos Islands, in sand at or near the coast, in association with *Bursera* and *Opuntia*. *Tiquilia galapagoa* is the only species of *Tiquilia* growing on Barrington, Brattle, Daphne,

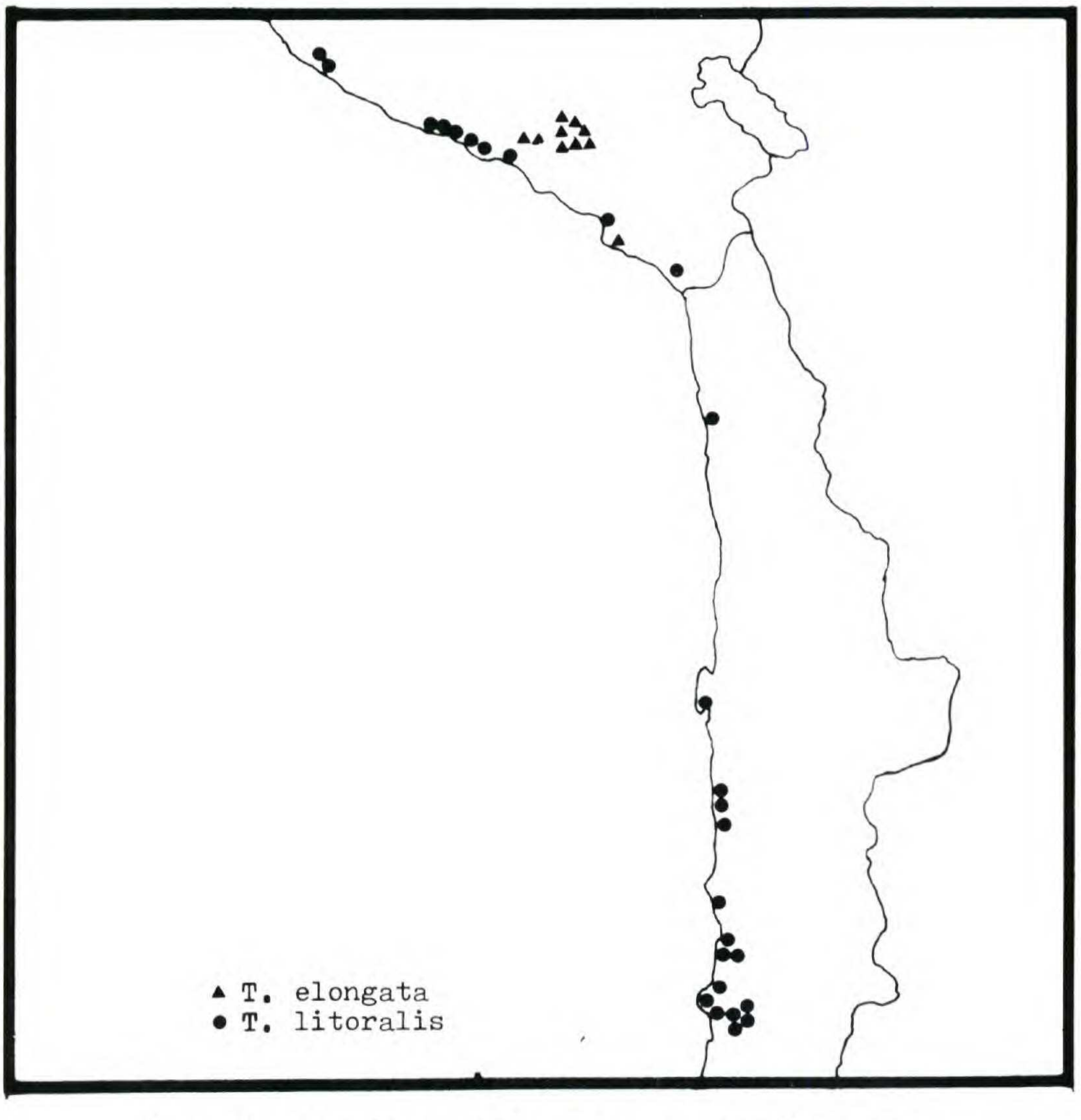

Figure 28. Distribution of *Tiquilia elongata* and *T. litoralis*.

Hood, Indefatigable, Jervis, and South Seymour Islands. It grows on Albemarle and Chatham Islands where *T. darwinii* also occurs, the two species sometimes growing together, and on James Island where *T. darwinii* and *T. nesiotica* are also found.

This species flowers January through December.

Tiquilia galapagoa resembles *T. paronychioides* in its granular nutlets, but differs from that species in its smaller leaves and corollas; its stamens being adnate equally to the corolla tube; its more deeply cleft styles; and its nutlets with narrower attachment scars broadening apically and basally. It is the only Galapagoan species with dull, granular nutlets, the other species having nutlets which are smooth and shiny.

Because of confusion in typification, this taxon has been known as *Coldenia fusca* (Howell, 1937; Wiggins & Porter, 1971). Thanks to recent research by Duncan Porter, who called this investigator's attention to the correct types of *Galapagoa darwinii* and *G. fusca,* this problem can be resolved (See also Porter, 1977).

Examination of the types of *Galapagoa darwinii* and *G. fusca* shows clearly that they are the same. An annotation by J. T. Howell on the holotype of *G. fusca* states that it corresponds with *G. darwinii.* Since *G. darwinii* is the first described, *G. fusca* is a synonym of that taxon; therefore another name is needed for the taxon previously known as *G. fusca.* Using the types designated by Howell (1937), this author had called *Coldenia galapagoa* J. T. Howell a synonym of *Galapagoa fusca,* since it represented a slight variation, with characters which intergraded with *G. fusca.* With *G. fusca* now a synonym of *G. darwinii,* the remaining available name is *Coldenia galapagoa.*

26. **Tiquilia nesiotica** (J. T. Howell) A. Richardson, Sida **6:** 236. 1976.

Coldenia conspicua J. T. Howell, Proc. Calif. Acad. IV. **12:** 105, 106. 1937. TYPE: **Ecuador:** GALAPAGOS ISLANDS. NW side of Bartholomew Island, 14 June 1932, *Howell 10059* (Holotype, CAS! Isotypes, CAS! F! GH! NY! US!). Not *C. conspicua* I. M. Johnston, 1935.

Coldenia nesiotica J. T. Howell, Proc. Calif. Acad. IV. **22:** 237. 1941. *Nom. nov.* based on *Coldenia conspicua* J. T. Howell.

Low spreading or suberect cinereous bushes 3.0–4.0 dm. tall; caudices to 7.0 mm. thick; older stems woody with brown bark; young stems with retrorsely and antrorsely appressed or spreading hairs to 0.4 mm. long. Leaf blades (Figure 8D) ovate-acute, 2.3–4.0 mm. long, 1.0–2.3 mm. broad, marginally entire; upper surfaces with antrorsely appressed hairs to 0.5 mm. long and sparse antrorsely inclined bristles to 7.0 mm. long, midrib plicate, lateral veins usually indistinct; lower surfaces with spreading and antrorsely inclined and appressed hairs along the prominent midrib; petioles trullate to ovate, sometimes filiform distally, 1.0–2.8 mm. long, densely ciliate, the abaxial surfaces with dense antrorsely appressed hairs, becoming sparsely pubescent or glabrate. Flowers solitary and axillary, or in small ebracteate groups of 2 or 3 with the leaf clusters. Calyces persistent, 1.5–2.0 mm. long, with dense spreading and antrorsely inclined hairs to 0.4 mm. long, and bristles to 0.7 mm. long apically; lobes 5, equal, subulate, free ca. 1/2 the

length. Corollas white, 2.5–3.0 mm. long, without appendages; the buds villous. Stamens included, unequal, adnate equally to the corolla tubes ca. 3.0 mm. above the base. Styles 1.5–1.9 mm. long, cleft to the base or within 0.3 mm. of the base, attached apically to the nutlets. Nutlets (Figure 10L) black, shiny, smooth, 0.7–0.8 mm. tall, 0.3–0.5 mm. broad, 0.4–0.6 mm. thick dorsi-ventrally, the attachment scar nearly the full length. Chromosome number, not known.

DISTRIBUTION: Limited to two adjacent islands of the Galapagos Archipelago, Bartholomew and James Islands.

Reported flowering times are February and June.

Tiquilia nesiotica has a superficial vegetative resemblance to *T. galapagoa*. It is most easily distinguished from that species by its smooth nutlets which are thicker dorsi-ventrally than broad. It is most closely related to *T. darwinii,* which also has smooth nutlets, and can be distinguished from that species by its larger leaves with spreading, inclined, and appressed hairs; larger corollas without appendages; included stamens; and the nutlets which are deeper dorsi-ventrally than broad.

27. **Tiquilia darwinii** (Hooker f.) A. Richardson, Sida **6:** 236. 1976.

Galapagoa darwinii Hooker f., Trans. Linn. Soc. London **20:** 196, 197. 1847. TYPE: **Ecuador:** GALAPAGOS ISLANDS. Chatham Island, Sep. 1835, *C. Darwin s.n.* (Lectotype, CGE, Mus. Henslow!).

Galapagoa fusca Hooker f., Trans. Linn. Soc. London **20:** 197. 1847. TYPE: **Ecuador:** GALAPAGOS ISLANDS. Charles Island, Sep. 1835, *C. Darwin s.n.* (Holotype, CGE, Mus. Henslow!).

Coldenia darwinii (Hooker f.) A. Gray, Proc. Am. Acad. **5:** 340, 341. 1862.

Coldenia fusca (Hooker f.) A. Gray, Proc. Am. Acad. **5:** 341. 1862.

Tiquilia fusca (Hooker f.) A. Richardson, Sida **6:** 236. 1976.

Prostrate, cinereous and brittle, forming mats to 10.0 dm. across; caudices to 11.0 mm. thick; older stems woody with whitish bark; young stems with antrorsely appressed or spreading hairs to 0.6 mm. long. Leaf blades (Figure 8E) obovate to ovate or elliptical, 2.0–2.7 mm. long, 1.2–1.5 mm. broad, marginally entire; upper surfaces with antrorsely appressed fine hairs to 0.2 mm. long and thick bristles to 1.1 mm. long, midrib plicate, lateral veins usually indistinct; lower surfaces more dense with antrorsely inclined hairs, the thickened midrib prominent; petioles trullate, occasionally filiform distally, 1.2–1.5 mm. long, densely ciliate, the abaxial surface

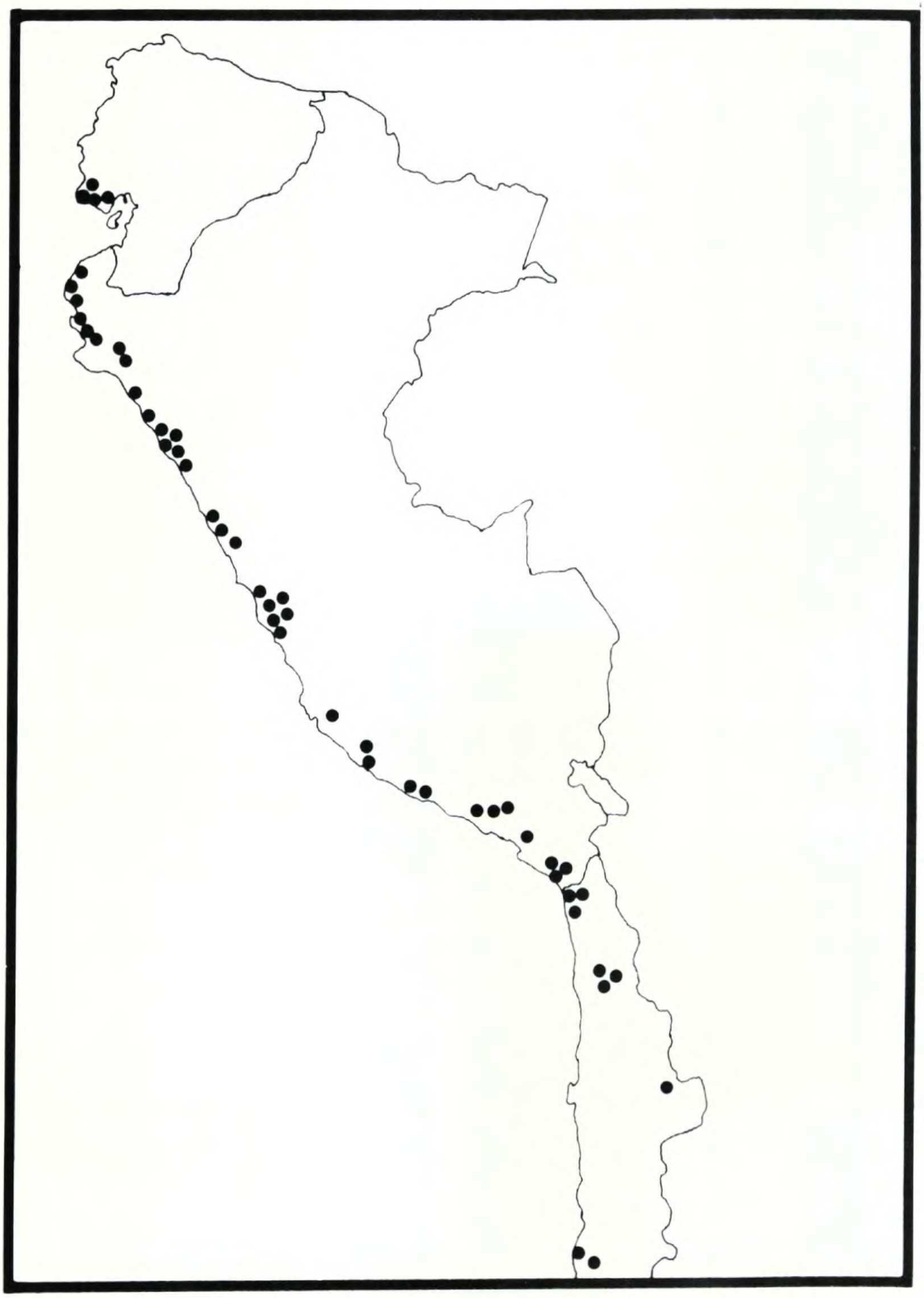

Figure 29. Distribution of *Tiquilia paronychioides.*

with dense antrorsely appressed hairs when young, becoming sparsely pubescent or glabrate. Flowers solitary and axillary, or in small ebracteate groups of 2 or 3 with the leaf clusters. Calyces persistent, 1.4–1.8 mm. long, with fine antrorsely appressed hairs and few stout bristles to 0.3 mm. long, denser distally; lobes 5, subequal, narrowly ovate to subulate, free ca. 1/2 the length; the fused bases usually forming 4 cups enclosing the nutlets. Corollas whitish, 1.3–1.7 mm. long; the buds villous. Stamens extending to the limb or slightly beyond, subequal, adnate equally to the corolla tubes ca. 0.2 mm. above the base, the veins below stamen attachments with small unialate wings. Styles 0.8–1.4 mm. long, cleft to the base or within 0.2 mm. of the base, attached apically to the nutlets. Nutlets (Figure 10M) black, shiny, smooth or minutely granular, 0.6–0.8 mm. tall, 0.3–0.5 mm. broad, the attachment scar nearly the full length, enlarging slightly apically and basally. Chromosome number not known.

DISTRIBUTION: Rather broadly distributed on the Galapagos Islands, on Abingdon, Albemarle, Bartholomew, Blindloe, Charles, Chatham, and James Islands, usually in coastal sands. It is the sole member of the genus on some of the smaller islands but more often shares an island with *T. galapagoa* and/or *T. nesiotica.*

Reported flowering times are February through June, August, and September.

Tiquilia darwinii is most closely related to *T. nesiotica,* both species having smooth, shiny nutlets. It is distinguished from that species by its smaller leaves with all under-surface hairs antrorsely appressed; its smaller, appendaged corollas; and its nutlets with ca. equal dimensions dorsi-ventrally as broad.

EXCLUDED TAXA

Coldenia glabra Phil., Anales Univ. Chile **90:** 229. 1895. TYPE: **Chile:** ATACAMA. Near Caldera, Sep. 1885, *R. Philippi s.n.* (Holotype, SGO!).

Coldenia phaenocarpa Phil., Anales Mus. Nac. Hist. Nat. Chile **2:** 55. 1892. TYPE: **Chile:** TARAPACÁ. Near Calcalhuay, 28 Jan. 1886, *R. Philippi s.n.* (Holotype, SGO!).

Coldenia succulenta Peter, Abh. Königl. Ges. Wiss. Göttingen, Math.-Ph. Kl. **13:** 90. 1928. TYPE: **Tanganyika:** Near Mkomasi, 6 Jun. 1915, *Peter 10857* (Holotype, B!).

= **Heliotropium curassavicum** L., Species Plantarum 130. 1753.

Lithospermum aggregatum Ruiz & Pavon, Prodromus et Flora Peruviana et Chilensis **2:** 4. 1799. TYPE: **Peru:** HUÁNUCO AND JUNÍN. Huánuco and Tarma, not seen. The following herbaria, upon inquiry, reported that the type is not in their possession: BM, F, GH, MA, OXF, and US. The description is too sketchy to evaluate. No species of *Tiquilia* are known from the type locality, which is not typical *Tiquilia* habitat.

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